# Bottom fish assemblages at the shelf and continental slope off East Greenland

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# Journal of Northwest Atlantic Fishery Science

Scientific publications by ICNAF and NAFO have been in existence since ICNAF began in 1949 with the ICNAF Special Publication series dealing with proceedings of scientific symposia. The *ICNAF Research Bulletin* was started in 1964 to provide a means of publishing results of scientific research relevant to ICNAF. The *ICNAF Research Bulletin* was terminated in September 1979 after the issue of Number 14. The first volume of the NAFO *Journal of Northwest Atlantic Fishery Science* was published in December 1980, after NAFO came into force replacing ICNAF in 1979.

The Northwest Atlantic fisheries have a rich history, and a great deal of research has been sponsored and encouraged by NAFO and its predecessor ICNAF. NAFO has been a leader amongst international organizations in the application of science to fishery management and in the regulation of fisheries in areas beyond national jurisdiction. In accordance with its mandate to disseminate information on fisheries research to the scientific community, the Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fishery Science*, which contains peer-reviewed primary papers, and *NAFO Scientific Council Studies*, which contains unrefereed papers of topical interest and importance to the Scientific Council. Lists of these and other NAFO publications are given on the back of this issue.

## Editorial Policy

The Journal provides an international forum for the primary publication of original research papers, with emphasis on environmental, biological, economic and social science aspects of fisheries and their interactions with marine habitats and ecosystems. While the Journal is intended to be regional in scope, papers of general applicability, and methodological and review papers, irrespective of region, are considered. Space is available for notes and letters to the editor to facilitate scientific discussion of published papers. Both practical and theoretical papers are eligible. All papers are peer-reviewed to determine their suitability for primary publication. Associate Editors arrange for the peer-reviews and ensure that the papers accepted for publication meet the high standards required for the Journal. Manuscripts approved for publication are accepted with the understanding that they are not copyrighted, published or submitted elsewhere except in abstract form. There are no page charges.

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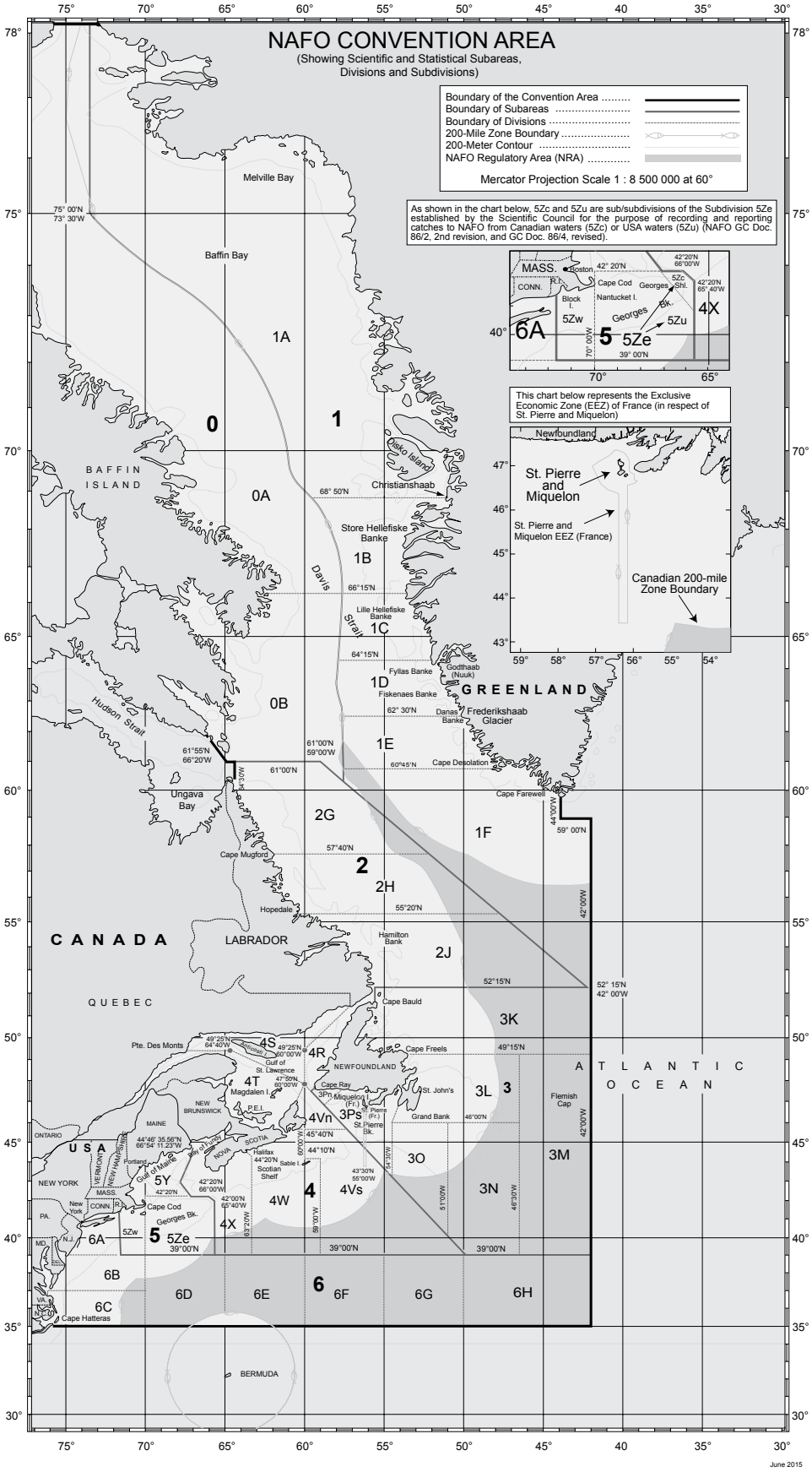
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As shown in the chart below, 5Zc and 5Zu are sub/subdivisions of the Subdivision 5Ze established by the Scientific Council for the purpose of recording and reporting catches to NAFO from Canadian waters (5Zc) or USA waters (5Zu) (NAFO GC Doc. 86/2, 2nd revision, and GC Doc. 86/4, revised).
This chart below represents the Exclusive Economic Zone (EEZ) of France (in respect of St. Pierre and Miquelon)
St. Pierre and Miquelon
St. Pierre and Miquelon EEZ (France)
Canadian 200-mile Zone Boundary
Newfoundland
Melville Bay
Baffin Bay
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Disko Island
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Store Hellefiske Banke
Lille Hellefiske Banke
Davis Strait
Godthaab (Nuuk)
Fyllas Banke
Fiskenaes Banke
Danas Banke
Frederikshaab Glacier
GREENLAND
Hudson Strait
Ungava Bay
Cape Desolation
Cape Farewell
Cape Mugford
Hopedale
CANADA
LABRADOR
QUEBEC
Hamilton Bank
Cape Bauld
Pte. Des Monts
Gulf of St. Lawrence
Cape Ray
Cape Freels
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St. Pierre (Pt.)
St. Pierre Bk.
Grand Bank
Flemish Cap
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NEW YORK
VERMONT
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6H
June 2015

# Foreword

The Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fisheries Science*, containing peer-reviewed primary literature detailing original research of relevance to fisheries science and management in the northwest Atlantic Ocean. Articles are published electronically under a Creative Commons (Canada) 2.5 license, and are freely available at http://journal.nafo.int. NAFO Scientific Council has resolved to produce annual bound print volumes and these represent a compilation of the web based articles published throughout the year. Additionally, the journal supports the use of digital object identifiers (doi) for electronic media and encourages others to support this initiative.

As always, this volume of the journal covers a range of topics representing ongoing research in the northwest Atlantic, including fishers behavior, planktonic distribution and various aspects of fisheries ecology.

In my final comments as General Editor of the journal, I would like to extend my thanks to all the authors who submitted works during 2015, to the Associate Editors and reviewers who make production of the journal possible, and to Alexis Pacey, publications manager at the NAFO Secretariat for her support and assistance over the past five years.

December 2015

Neil Campbell
General Editor,
*Journal of Northwest Atlantic Fishery Science*

# Contents

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# The Value of Captains' Behavioral Choices in the Success of the Surfclam (*Spisula solidissima*) Fishery on the U.S. Mid-Atlantic Coast: a Model Evaluation

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POWELL, E. N., J. M. KLINCK, D. M. MUNROE, E. E. HOFMANN, P. MORENO, and R. MANN. 2015. The Value of Captains' Behavioral Choices in the Success of the Surfclam (*Spisula solidissima*) Fishery on the U.S. Mid-Atlantic Coast: a Model Evaluation. *J. Northw. Atl. Fish. Sci.*, **47:** 1–27. doi:10.2960/J.v47.m701

## Abstract

The response of the surfclam *Spisula solidissima* to warming of the Mid-Atlantic Bight is manifested by recession of the southern and inshore boundary of the clam's range. This phenomenon has impacted the fishery through the closure of southern ports and the movement of processing capacity north, impacts that may require responsive actions on the part of fishery captains to mitigate a decline in fishery performance otherwise ineluctably accompanying this shift in range. The purpose of this study was to evaluate options in the behavioral repertoire of captains that might provide mitigation. A model capable of simulating a spatially and temporally variable resource harvested by fleets of boats landing in a number of homeports was created. The model includes characterization of each vessel in terms of economics and vessel performance. The model assigns to each vessel a captain with defined behavioral proclivities including the tendency to search, to communicate with other captains, to take advantage of survey data, and to integrate variable lengths of past history performance into the determination of the location of fishing trips. Each captain and vessel operate independently in the simulation providing a spatially and temporally dynamic variability in fishery performance. Simulations showed that a number of behaviors modestly varied performance. Use of survey data and occasional searching tended to increase performance. Reliance on an older catch history tended to reduce performance as did frequent searching. However, in no simulation was this differential large and the differential was little modified by the contraction in the surfclam's range. Simulations showed that the population dynamics of the clam and the low fishing mortality rate imposed by the Fishery Management Plan permit near optimal fishing performance based on a few simple rules: choose locations to fish that minimize time at sea while permitting the landing of a full vessel load; base this choice on the most recent catch history for the vessel. Simulations suggest that the performance of the fishery is primarily determined by surfclam abundance and the location of patches that control LPUE at small geographic scales. Constraints imposed on fishery performance by port location and vessel size far exceed limitations or ameliorations afforded by modifications in the behavior of captains.

*Keywords*: captain, skipper, behavioral choice, surfclam, *Spisula*, fishery model, fishery economics, fishing practice

## Introduction

The Atlantic surfclam, *Spisula solidissima*, sustains one of the largest shellfish fisheries on the east coast of the U.S. The fishery is operated under a fixed quota distributed to shareholders under an ITQ (individual transferable quota) system (Adelaja *et al.*, 1998; McCay *et al.*, 2011). Surfclams are sensitive to bottom water temperatures above about 21°C (Weinberg, 2005; Munroe *et al*., 2013). As a consequence, warming of the Mid-Atlantic Bight (Scavia *et al*., 2002; Jossi and Benway, 2003; Narváez *et al.*, 2015) has resulted in a range contraction for this species since the mid-1990s (Weinberg *et al.*, 2002, 2005; Weinberg 2005) characterized by a large-spatial-scale mortality event at the southern boundary of the range (Kim and Powell, 2004; Narváez *et al.*, 2015) driving the southern boundary northward and offshore. A compensatory northward shift at the leading edge has not occurred, although a modest offshore range extension off New Jersey is well-documented (*e.g.*, Weinberg *et al.*, 2005). A consequence of this shift in range is a contraction of the region supporting much of the fishery from the southern region off Maryland and Virginia to the more northerly region off New Jersey (NEFSC, 2013).

Obvious impacts on the fishery from this range contraction include the movement of processing plants northward, the shift of vessels from southerly ports northward, and the focus of heaviest fishing pressure in a smaller region. These dynamics, both economic, managerial, and biological, influenced the development of a management strategy evaluation (MSE) model of the surfclam industry (see Mahévas and Pelletier, 2004; Baudron *et al*., 2010; Bastardie *et al*., 2010; Miller *et al*., 2010 for other examples of MSE models). One of the dynamic aspects of this evaluation is the need to understand how differences in vessel characteristics and locations of homeports interact with behavioral choices made by captains in determining the degree of success of fishing trips. The approach to fishing implemented by the fleet captains is an important ingredient in the dynamic of any fishing industry (Dorn, 1998, 2001; Gillis *et al*., 1995a,b; Powell *et al*., 2003a,b). How these choices interact with changing dynamics of the stock and differences in fishing vessel size represent both an important component of the economic response by the fishery (Lipton and Strand, 1992) and an important component of an MSE. The purpose of this contribution is to utilize an MSE model for surfclams as a vehicle to investigate how ongoing climate change inducing a change in geographic distribution of the stock influences the success of the fishery as modulated through the range of choices potentially available to the vessel captains as they execute their fishing trips.

## The Model - SEFES (Spatially-explicit Fishery Economics Simulator)

### Overview

SEFES is a model capable of simulating a spatially and temporally variable resource (in this case, surfclams) harvested by fleets of boats landing in a number of homeports. The structure of SEFES is depicted in Fig. 1. Boats and processing plants are the active agents in the model. The boats are attached to specific processing plants and land catch at dedicated ports. The boat may have varying characteristics such as different speeds, harvest capacities, and costs. Each boat is controlled by a captain with specified characteristics that determine where and how efficiently the boat harvests the resource. SEFES is relatively unique in permitting each captain and vessel to identify a new fishing location for each trip based on specified vessel, behavioral, and stock characteristics (see Bockstael and Opaluch, 1983; Béné, 1996; Hutton *et al*., 2004 for examples of other models including behavioral choice). Boats move around the domain and harvest clams based on decisions by the captain as constrained by the operating characteristics of the boat, such as speed, maximum allowed time at sea, and imposed harvest quota. Each port has a processing plant that purchases the harvested clams, providing income for the boats, and distributes quota to each boat on a weekly schedule.

The spatial domain is partitioned into rectangular cells ten minutes (about 10 nautical miles (nm) in the modeled region) on a side. Within each cell, the surfclam population is described in terms of surfclams $m^{-2}$ per 1-cm size class. The number and size distribution of surfclams is modified over time in response to different biological and fishery processes. Surveys are conducted annually to determine the size and distribution of the population. A management module imposes reference points and calculates the allowable biological catch (ABC) used to set the harvest quotas for the next year.

The basic units in the model are SI with time in seconds, distance in meters, and weight in kilograms. For convenience, commonly-used units are used to set various characteristics, such as specifying boat speed in knots (kt). Calendar software is included to convert model days to calendar dates (Julian days). This capability allows the model to determine the beginning of a month or a year and to determine the day-of-the-week for a given event. Being able to identify the month allows the model to impose known seasonal variability such as weather and surfclam yield (meat weight for a given clam length). Being able to identify the day of the week permits fishing trips to be

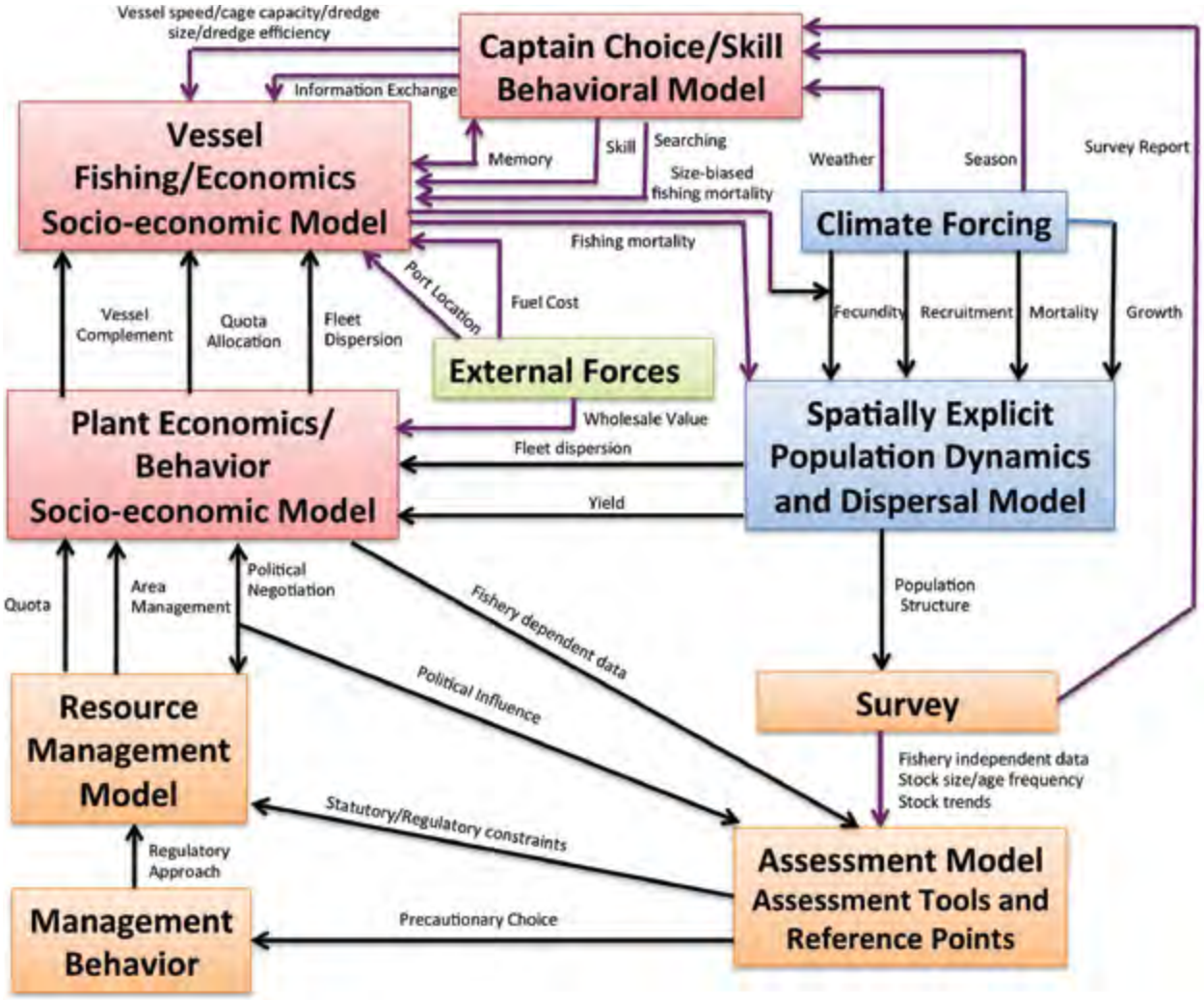


Fig. 1. SEFES model structure showing population dynamics components in blue, survey and management components in orange, external forces in green, and industry structure and function in pink.

organized with respect to known processing schedules of the processing plants. The length of a simulation is controlled by a start and end calendar date. For these simulations the first day is set arbitrarily at 1 January 2000 and the end date is set arbitrarily at 1 January 2051 which gives a 51-year simulation (2000–2050).

**Domain and Geometry Configuration**

The model domain is a rectangular distribution of square cells 10 minutes of latitude by 10 minutes of longitude (Fig. 2). The north-south size of the cell is 10 nm. The east-west size of the cell is fixed at some width determined by the central latitude of the grid. The domain investigated in this paper is the Mid-Atlantic Bight (MAB) off the east coast of the US. The east-west extent of the domain has 17 cells across-shelf in the south and alongshore in the north to represent the transition from a quasi north-south trending shoreline south of Hudson Canyon to an east-west shoreline north of it. The north-south extent of the domain has 26 cells from Long Island south. The central latitude for these cases is 38ºN. For convenience, this model domain has the MAB rotated slightly counterclockwise to remove the northeastward trend south of Long Island, but this slight distortion of the domain has a negligible effect on model processes. Thus, the basic domain is a 17 cell by 26 cell grid wherein each cell is identified by a pair of numbers (*ix, iy*) which count the number of cells eastward (*ix*) and northward (*iy*) from the southwest corner of the model grid.

A mask is imposed on the model domain which identifies each cell as being land, water uninhabited by surfclams, or water inhabited by surfclams. This mask is static, being

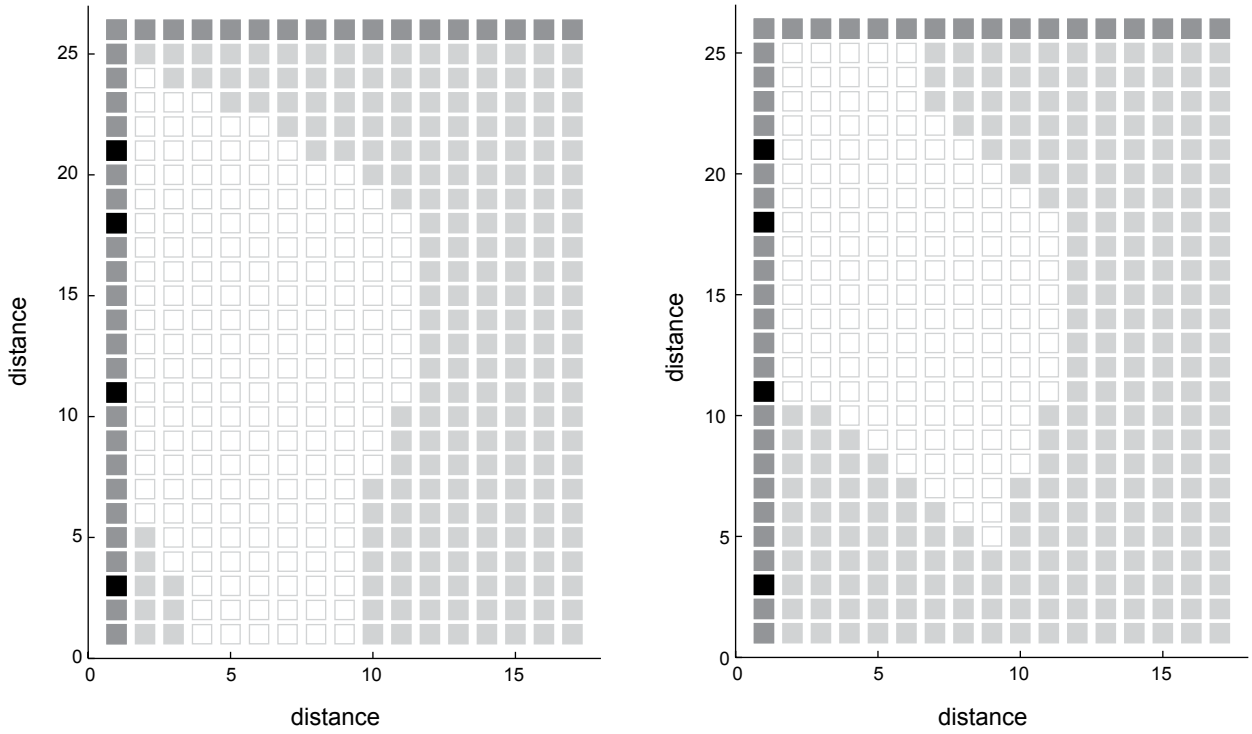


Fig. 2. Left, the domain used to simulate conditions present during the 1990s. Right, the domain used to simulate conditions present during the 2000s. Darkest squares show the position of 4 ports, from north to south Pt. Pleasant, New Jersey; Atlantic City, New Jersey; Ocean City, Maryland; and Norfolk, Virginia. Medium gray squares identify the remainder of the coast line. Light gray squares identify water locations where surfclams are not found. The fishable domain encompasses the open squares. Note that the domain has been rotated for convenience to remove the northeast-southwest trend of the U.S. east coast south of Long Island without changing the dimensions of the 10-minute squares or the distances between ports and fishing grounds.

defined at the beginning of a simulation. Ports are specified to be in certain land cells. For convenience, processing plants and ports are colocated. For the simulations in this paper, four ports are included in the approximate locations of Norfolk, Virginia; Ocean City, Maryland; Atlantic City, New Jersey; and Pt. Pleasant, New Jersey (Fig. 2). These ports represent the primary ports for landing surfclams over the time period of interest. In the 2000s, the majority of the harvest in the Mid-Atlantic Bight was landed in the ports of Atlantic City and Pt. Pleasant. In the 1990s, the Ocean City port was also important and, earlier in the fishery (1980s), the port of Norfolk was important. NEFSC (2003, 2013) show the distribution of landings over time, including the northward shift in effort that resulted in the sequential closure of the Norfolk and Ocean City homeports.

## Boat Details

### *Operational Limits*

Activity by boats is monitored hourly. Boats are permitted three activities. They can wait at the homeport, steam to and from a fishing location, or fish. At the beginning of every hour, the current activity of the boat is determined, some action occurs, and an activity for the next hour is set. These actions are managed by three hour counters: *HomeWait*, *TripTime*, and *FishTime* (Table 1). As an action begins, these counters are set to the correct value for a boat to 1) wait at the dock for an opportunity to go fishing, 2) steam from the port to the fishing location or return, or 3) fish.

### *Operating Characteristics*

Vessel characteristics were obtained from interviews in 2012 with industry representatives and boat owners and operators. Although a spectrum of detailed differences exist among vessels in the surfclam fleet, these vessels can be grouped crudely into small (~40-cage[1] capacity), medium (~80-cage capacity), large (~120-cage capacity), and jumbo (~160-cage capacity). For this study, two common vessel types were compared, small and large. The large vessel has 3 times the capacity of the small vessel. Simulations were run with an equivalent fishing power for each port and vessel type. Accordingly, all ports had the same number of vessels of a given size and simulations using small vessels used three times as many small vessels as large vessels. Total fishing power in the simulations

[1] 1 cage = 32 surfclam bushels = 1.7 $m^3$; 1 surfclam bushel = 53 L.

was similar to that observed in today's Mid-Atlantic Bight fishery. Thus, 20 large vessels, five per port, and 60 small vessels, 15 per port, were specified.

Each boat in the model has a number of characteristics set at the beginning of the simulation. The following characteristics were specified for the small vessel: steaming speed, 8 kt; maximum on-deck processing capacity, 6 cages $hr^{-1}$; dredge width, 2.6 m; dredging speed, 3 kt. The same characteristics for the large vessel were: steaming speed, 12 kt; maximum on-deck processing capacity, 20 cages $hr^{-1}$; dredge width, 3.8 m; dredging speed, 3 kt.

***Boat Economics***

Each boat is given a homeport where catch is landed and derives quota from a specified processing plant colocated for convenience at that homeport. Vessel economic data were obtained from MAFMC (1988; see also Weninger and Strand, 2003) and updated by interviews in 2012 with industry representatives and vessel operators. Costs for certain activities are calculated in terms of fuel used and crew costs. Fixed costs of boat and gear maintenance as well as capital costs of the boat are included. For these simulations, the following were specified (small vessel, large vessel): fixed costs ($1,579 $d^{-1}$, $1,165 $d^{-1}$); crew share as fraction of catch revenue (0.2, 0.2); boat share as fraction of catch revenue (0.15, 0.15); gear maintenance ($1,500 $trip^{-1}$, $1,000 $trip^{-1}$); fuel use steaming (30 gal $hr^{-1}$, 50 gal $hr^{-1}$); fuel use fishing (45 gal $hr^{-1}$, 80 gal $hr^{-1}$). Note that the higher fuel use while fishing occurs because these vessels use hydraulic dredges and the water pump is engaged while dredging. Note that the higher fixed costs and costs of gear maintenance for the smaller vessels incorporate the average older age of the vessel in service. For these simulations, the ex-vessel value of landings was set at $12 (surfclam bu)$^{-1}$ and the price of fuel was set at $4 $gal^{-1}$. As many of the economic values used are temporally variable, economic results are best assessed on a relative basis by comparing outcomes between ports, vessel sizes, and captains.

**Captain Descriptors**

Information describing a captain's decision-making process when planning a fishing trip, constraints imposed by landing deadlines, and the captain's approach to information acquisition on clam abundance were obtained from interviews of vessel captains supplemented by interviews with other industry representatives and the authors' own extensive experiences.

***Captain's Memory***

The captain controls where the boat fishes. Each captain retains the memory of past fishing trips which influences which 10-minute square is targeted for the next fishing trip. This memory log contains an expected LPUE (landings per unit effort) specified in cages per hour fishing for every fishable 10-minute square in the domain. At the beginning of the simulation, the memory of each captain

Table 1. Flow diagram for time stepping through the various activities carried out by a fishing vessel. Boat status is checked every hour.

if Current State = = WAIT

if HomeWait > 0: Keep waiting and decrement HomeWait by 1 hr.

if HomeWait = 0: The next action depends on the weather.

if Weather ≥ boat type: The weather is too bad. Wait in port for 4 days.
Set HomeWait to 96 hr (4 days).

if Weather < boat type: Then fishing is possible. Update the weekly quota if it is a new week. If the remaining weekly quota is at least 90% of the boat capacity, then choose a fish location and go fishing. Set the activity to TRAVEL. Calculate the TripTime and FishTime for this fishing trip.

if Current state = = TRAVEL

if boat is at the destination:

if FishTime > 0: The boat is at the fishing ground. Set activity to FISH.

if FishTime = 0: The boat is at the processing plant. Set activity to WAIT and set HomeWait to 12 hr. Sell the harvest to the plant and calculate cost and revenue. Update the captain's history for the 10-minute square just fished. Share current catch information with appropriate captains (if active). If boat is not at destination: Continue to travel. Decrement TripTime by 1 hr.

if Current State = = FISH

if FishTime = = 0: Fishing is over. Set activity to TRAVEL; the destination is the plant.

Calculate the travel time and set TripTime.

if FishTime > 0: Decrement FishTime by 1 hr and continue fishing.

contains the LPUE that would be experienced by his boat for all 10-minute squares based on the square's initial surfclam abundance. That is, initially, all captains have omniscient information. At the end of each fishing trip, the catch history in the captain's memory log is updated for that 10-minute square. In this way the captain's memory of the entire domain degrades over time as the surfclam population changes independently of the captain's experience and, therefore, updated memory of it. The captain uses his memory of LPUE to choose a 10-minute square for fishing.

Each captain has a memory weight factor that is used to update the memory log. After fishing in a certain 10-minute square and returning to port, the LPUE for that trip is used to update the information in the captain's memory log based on a memory factor (*f*) that is a fraction indicating the weight placed on past information; *1-f* is the weight placed on the most recent LPUE. If the fraction is 0.5, then the memory retained is the average of the previously stored and just obtained LPUEs. If the fraction is 1, then the old information is retained and the new information is ignored. If the fraction is 0, then the old information is forgotten. Of the captain's characteristics, only the captain's memory, but not the memory factor, varies over time during the simulation.

Observations and interviews determined that captains routinely keep detailed logs of their fishing activities, both handwritten and in electronic format, so that an extensive history of the fishing experience is routinely available to most captains in the fleet. The value of this information can be expected to degrade over time as fishing, recruitment, and natural mortality impact the distribution and abundance of the stock. Certain captains rely more heavily on a longer term integration of their fishing experiences than do others. For simulations discussed here, captains were assigned memory weights of 0.2 and 0.8 or 0.98 and 0.99 (Fig. 3). Thus, certain captains' memories were biased towards new or old information, respectively. Responsive captains, given a memory weight of 0.2 or 0.8, based fishing decisions on performance within the previous 1 to 6 weeks depending on the value of *f* and the number of trips taken per week. Obdurate captains, given a memory weight of 0.98 or 0.99, based fishing decisions on performance over a much longer period of time (7 months to well over 1 year). The responsive captain is considered an average captain in today's fleet and is used subsequently as a point of comparison to captains exercising alternative behaviors.

***Captain's Idiosyncrasies***

The captain is conferred certain degrees of boldness, inquisitiveness, skill, and loquacity (Table 2).

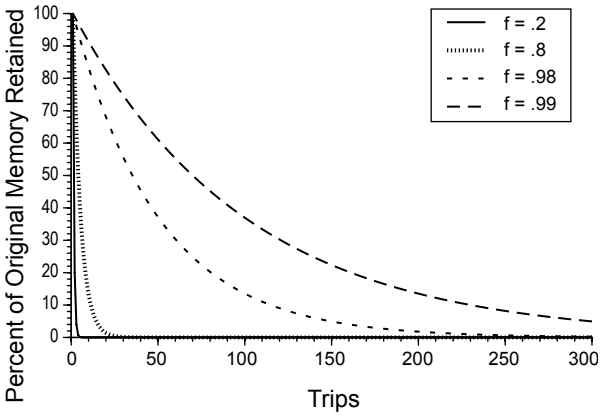


Fig. 3. The fraction of original memory retained by a Captain given a defined weighting (*1-f*) of new information from each trip relative to the Captain's previous memory for the four memory settings used in this study. As boats take one to two trips per week, the x-axis value multiplied by 2 is an estimate of the minimal number of elapsed days.

Skill, ranging between 1 and 10, determines how efficiently the captain conducts the fishing venture; that is, skill determines the fraction of time on the fishing ground during which the dredge is actively fishing. For these simulations, a captain with low skill fishes for 75% of the time while on the fishing ground whereas a captain with high skill fishes 100% of the time.

Boldness determines if the captain's behavior includes searching behavior. In the current model, a timid captain never searches, a bold captain searches every time he leaves port, while the confident captain searches about 20% of the time, about once a month. In the surfclam fishery, vessels are expected to return to the dock within 48 hr during the warm months of the year. Thus, captains have limited time to search. Accordingly, in the model, when searching, the captain targets a random square within a six-hr steam of the homeport regardless of his memory of past LPUE performance in that cell. Thus the bold captain, in effect, fishes randomly among a selection of 10-minute squares irrespective of the catch and a confident captain does so also, but 80% less often.

Inquisitiveness indicates whether or not a captain uses the most recent survey results to update his knowledge of the expected LPUE for each 10-minute square. Indifferent captains do not use the survey results, whereas inquisitive captains use the most recent survey. The federal survey frequency for surfclams is once every three years (NEFSC, 2013) and the provision of survey data to the public in the form of fishermen's reports (*e.g.*, NEFSC, 1999, 2002) occurs within a few months of the survey. These reports provide the raw tow results for each station on the survey.

Table 2. Designations and definitions of captain's traits.

| | Captain Trait Designations and Definitions | | | | |
|---|---|---|---|---|---|
| Captain Type | Responsiveness | Skill | Boldness | Inquisitiveness | Loquaciousness |
| Responsive | Responsive<br>Memory=0.2,0.8 | Skilled<br>Time Fishing=100% | Timid<br>Never searches | Indifferent<br>Never uses survey | Taciturn<br>Communication probability=0 |
| Obdurate | Obdurate<br>Memory=0.98, 0.99 | Skilled<br>Time Fishing=100% | Timid<br>Never searches | Indifferent<br>Never uses survey | Taciturn<br>Communication probability=0 |
| Low Skill | Responsive<br>Memory=0.2,0.8 | Low Skill<br>Time Fishing=75% | Timid<br>Never searches | Indifferent<br>Never uses survey | Taciturn<br>Communication probability=0 |
| Bold | Responsive<br>Memory=0.2,0.8 | Skilled<br>Time Fishing=100% | Bold<br>Searches each trip | Indifferent<br>Never uses survey | Taciturn<br>Communication probability=0 |
| Confident | Responsive<br>Memory=0.2,0.8 | Skilled<br>Time Fishing=100% | Confident<br>Searches on 20% of trips | Indifferent<br>Never uses survey | Taciturn<br>Communication probability=0 |
| Inquisitive | Responsive<br>Memory=0.2,0.8 | Skilled<br>Time Fishing=100% | Timid<br>Never searches | Inquisitive<br>Uses survey | Taciturn<br>Communication probability=0 |
| Loquacious | Responsive<br>Memory=0.2,0.8 | Skilled<br>Time Fishing=100% | Timid<br>Never searches | Indifferent<br>Never uses survey | Loquacious<br>Communication probability=0.5 |

Thus, in these simulations, the inquisitive captain updates his memory every third year based on survey results.

Loquacity determines the tendency for a captain to share the results of his most recent trip with other captains. This propensity is invoked in the model in probabilistic terms. For these simulations, captains are either taciturn, so that information is never shared, or loquacious, so that the captain shares information to each other captain with a probability of 0.5.

Simulations were run with captains varying by only one trait relative to the standard, responsive captain. Thus, the responsive captain is responsive, skilled, timid, indifferent, and taciturn (Table 2). In contrast, the confident captain varies from this suite of traits in only one way, he is confident rather than timid; in other words, he searches occasionally. However in all other traits, he is identical in behavior to the responsive captain (Table 2). Similarly, the loquacious captain is identical to the responsive captain in all but one trait; he is loquacious rather than taciturn.

**Processing Plant**

The two major functions of the processing plants are to buy clams from the boats and to set the weekly quota for the fleet of boats fishing for the plant. Surfclam fishing vessels are strictly tied to plants, so that no vessels fish for more than one plant. The weekly quota controls the number of fishing trips per week. The surfclam fishery is an ITQ fishery. For the purposes of this study all plants are assumed to own an equivalent number of ITQ shares and to have fleets with equivalent fishing powers. Consequently, the quota is distributed evenly as a consequence of the even distribution of ITQ shares.

The harvest quota for the year is calculated at the time of the November survey of the previous year. On the first of January, this quota is distributed among the processing plants in proportion to the fraction of the total fishing power that is represented by the fleet that is attached to that plant. Each plant distributes its fraction of the total quota to its fishing boats in proportion to their hold size on a weekly basis. The weekly quota for a boat is limited to twice its hold size in order to limit fishing trips to no more than twice a week. This is consistent with the standard operating procedure in the surfclam industry. As much as possible, the weekly quota is distributed to boats in allocations equivalent to full hold capacity.

If the weekly quota for a boat averaged over the year is below twice its hold size, then the boat cannot complete

two trips per week over the entire year. In this case, the quota is shifted in the year so that the largest quota occurs in the months when meat yield is the highest. In the present model, the 20th week of the year has the largest yield. During this time, boats can take two trips per week to the extent that the number of total trips exceeds one trip per week each week of the year. Consequently, one-trip weeks are allocated to periods when yield is low. This maximizes the profit for the plants. The weekly quota is renewed at the beginning of the week, defined to be Sunday in the model.

The plants pay the boats \$12 (surfclam bu)$^{-1}$ for the landed surfclams. For the purposes of these simulations, all other plant economics are inconsequential to the outcome of the analysis and thus are not reported in this study.

**Weather**

Fishing may cease due to weather, primarily in the winter. Thus, weather was imposed as a factor for 6 months of the year (October–March). The frequency of different winter wind speeds was obtained from two NOAA meteorological buoys (NDBC 44008 over Nantucket Shoals and NDBC 44009 off Cape May). This wind analysis gave the fraction of time that boats of different sizes could fish. For the simulations here, weather of intensity 5, 4, 3, 2, 1, 0 occurs 5%, 10%, 15%, 20%, 30%, and 20% of the time, respectively. The higher weather index indicates higher winds.

Boats of increasing size have increasing boat indices that range from 1 to 4. The weather effect is imposed by restricting boats with an index less than the weather code from leaving port. In the model, during winter, the weather code for the current day is determined by a random draw and this determines which boats can fish. Boats already at sea are not affected by the current weather. Most fishing trips are at most two days long so this weather restriction on leaving port is effective without requiring, in the model, that boats at sea return to port in bad weather. For this study, small boats were given a weather code of 1 and large boats a weather code of 3. Thus, small boats have a 50% chance on any given day of leaving port in the winter; large boats have an 85% chance.

**Surfclam Biology**

***Initial clam distribution***

The initial surfclam distribution (clams m$^{-2}$ per size class) is calculated in two steps. A biomass for the total population is imposed as an initial condition for the simulation. This biomass is distributed among 10-minute squares as a total clam density (summed over sizes) using a negative binomial random distribution to create a patchy distribution over the 10-minute squares in which surfclams can exist. Then, a spatially-varying size distribution is used to distribute the surfclams in each 10-minute square into size categories. Patchiness is maintained subsequently by recruitment, as described in a later section.

The growth and mortality rates for the surfclam population are specified separately for different simulations so the originally specified population size-frequency and density distribution may be inconsistent with these parameters. The model initial conditions are adjusted by running the model for 100 years without fishing to allow the initial population to adjust to the chosen rates of growth, mortality, and reproduction. Fishing in each model run, therefore, begins with a virgin stock.

***Size and growth***

The clams are distributed in 18 length classes of 1-cm interval starting at 2 cm and extending to 20 cm. The average length for a size category is the average of the lengths on either edge of the box. So, for example, the first size category includes all clams between 2 and 3 cm in length and has an average length of 2.5 cm.

The average wet weight for the animals in each size category is calculated with an allometric relationship of the form

$$W = aL^b. \quad (1)$$

Parameter values come from Marzec *et al*. (2010).

A daily growth rate for each size class for each 10-minute square was calculated from the von Bertalanffy age-length relationship for that square:

$$L = L_\infty \left(1 - e^{-kA}\right) \quad (2)$$

where $L$ is length in mm and $A$ is age in years. $L_\infty$ is the largest length for the clam and $k$ (yr$^{-1}$) is the rate that the smallest clams grow. The von-Bertalanffy parameters were estimated from information provided by the federal surfclam survey (NEFSC, 2013; see also Munroe *et al*., 2013). The growth rate (length change per time) is determined for each size class by calculating the age of the clam at the smaller edge of the length box. Then the length of the clam one year younger is calculated from the von Bertalanffy relationship. The one year length change divided by the length change over the length of the box determines how quickly clams move from one box to the next.

Natural mortality is imposed once yearly using a specified instantaneous mortality rate $m$ that is the same across all size classes. Munroe *et al*. (2013) raise the issue of

increased mortality at old age, consistent with other bivalves (see Powell *et al*., 2012). However, the presently-accepted stock assessment model retains the constant mortality assumption consistent with Weinberg (1999). The present model follows the assessment approach.

Growth and mortality vary by 10-minute square. This is accomplished by specifying the values of $k$, $L_\infty$, and $m$ at the corners of the domain and assigning values to each 10-minute square by interpolation. In cases where a more complicated cross-shelf distribution is desired, values at the mid-points of the domain are also specified prior to interpolation. This permits latitudinal and cross-shelf variations in growth and mortality (Weinberg, 1999; Chintala and Grassle, 2001; Weinberg *et al.*, 2002; Munroe *et al*., 2013).

For the 1990s simulations, the mortality rate is isotropic and specified as 0.15 $yr^{-1}$. For the 2000s simulations, mortality rate increases from this rate southeasterly across the domain to reduce surfclam abundance at the southern and inshore extremes of the range, consistent with Weinberg (1999, 2005). The von-Bertalanffy parameterization results in higher growth rates, with $k$~0.26 $yr^{-1}$ in the 1990s, but relatively isotropic over the range. The 2000s values vary latitudinally from 0.25 $yr^{-1}$ in the south to 0.19 $yr^{-1}$ in the north and decline offshore to 0.15 $yr^{-1}$. $L_\infty$ varies latitudinally in both time periods with values from 150 to 164 cm in the 2000s and somewhat higher in the 1990s.

***Reproduction***

Surfclams recruit to the population one day per year, chosen arbitrarily to be October 1. The total number of recruits is calculated from the total population biomass. A stock-recruit relationship is not available for surfclams. Beverton-Holt parameters are estimated for the virgin stock from an input value for steepness, set at 0.8 for these simulations, following the method of Myers *et al*. (1999; see also O'Leary *et al*., 2011). Each year, total recruitment is calculated using the Beverton-Holt relationship and the total stock biomass. Interannual variability is imposed by obtaining a random factor that is applied to the total number of recruits. Recruitment is parsed out to each 10-minute square by adding individuals to the smallest size class (20 mm) based on a negative binomial distribution which makes the cell-wise recruit process patchy. The smallest size class used is consistent with juvenile growth rates that show that newly settled surfclams can reach 20 mm by the end of the settlement year (Chintala and Grassle, 1995; Ma *et al.*, 2006).

***Meat yield***

Meat yield for a surfclam depends on the time of year and the 10-minute square. Yield is measured as usable meat and is about 75% of the wet meat weight. As part of model setup, a yearly minimum and maximum yield is specified for an average market-size clam. The actual yield for a given fishing trip depends on the time of year since clam meats are heavier in late spring through early fall during the spawning season (Ropes, 1968; Jones, 1981; Spruck *et al*., 1995). A 5$^{th}$-order polynomial based on the day of the year provides a time-varying yield between 11 and 15 lb (surfclam bu)$^{-1}$. This yield curve was obtained from the industry who retain detailed records of yield as part of their economic planning. The meat weight for the clams of different sizes is determined from the allometric relation (equation 1). The weight of clam meat in a bushel is calculated from the number of clams of a given size in a bushel and the wet weight of the clams of that size, standardized to the yield curve using the weight and yield of a 150-mm clam.

**Choosing a Fishing Location**

A captain chooses a fishing location by the following rational processes based on his memory log. For those captains not searching, the captain calculates the time to steam from the port to each 10-minute square in turn. Then the captain calculates how many hours would be required to fill his boat based on his remembered LPUE. The captain chooses to fish in the square for which the fill time is least and the distance to the square shortest in order to minimize time at sea while returning to the dock with a full load. Interviews with industry representatives emphasize the time-at-sea criterion. The captain is assumed to know LPUE in whole cage units per hour. Thus, a number of 10-minute squares may have the same LPUE. Accordingly, the captain identifies one or more 10-minute squares that maximize LPUE and chooses among these for his next trip the 10-minute square nearest to port.

**Fishing Details**

The number of surfclams harvested during an hour of fishing is calculated from the area swept by the dredge, which depends on the tow speed and dredge width, the efficiency of the dredge, the size selectivity of the dredge, and the skill of the captain. In addition, the harvest is reduced if the harvest rate per hour exceeds the boat's handling capacity. The number of hours fished is determined by the time necessary to fill the vessel, as constrained by the allowed time on site given the steaming time to return to port. Vessel characteristics were obtained from vessel captains and industry representatives. Selectivity and efficiency relationships were obtained from the federal survey program (*e.g.*, NEFSC, 2013; see

Rago *et al.*, 2006 and Hennen *et al*. 2012 for additional details).

At the beginning of the fishing hour, if the total catch for the trip has reached the boat capacity or if the available time-at-sea has elapsed, then fishing stops and the boat returns to port (Table 1). Boat capacity is defined in terms of cages, a volumetric measure, whereas individual clams of varying sizes are caught by the dredge. Numbers are converted to volume based on the number of clams of various size classes per bushel. The number of clams per bushel for a given 1-cm size interval was obtained from direct counts of clams of known size landed in Atlantic City, NJ in 2012. Thus, each sized clam is associated with a volume occupied in the bushel, including clam plus void space, and the volumes summed to estimate the total cage volume provided by the dredge haul.

**Survey Details and the Annual Quota**

A complete survey of the surfclam population is conducted on November 1. This allows the survey to record the most recent recruitment event. The survey is perfect in that it uses the true clam density for each 10-minute square and samples every square. The survey determines the biomass of the fishable stock, specified for these simulations as all clams ≥12 cm. This size is consistent with industry dredge selectivity curves that show high catch efficiency for clams ≥12 cm (NEFSC, 2013). The stock survey uses a survey dredge that can be different from that used by the fishing boats in its efficiency and size selectivity. Up through the latest (2012) federal survey (NEFSC, 2013), that difference was significant in that selectivity of the survey dredge was dome shaped and smaller clams were caught more efficiently than with the industry dredge (NEFSC, 2013).

The total fishable biomass (*Fbio*) is used to set the annual quota based on two reference points, biomass at maximum sustainable yield ($B_{msy}$) and the fishing mortality rate, $F_{msy}$, yielding *msy* at $B_{msy}$. $F_{msy}$ was set to 0.15 $yr^{-1}$ (NEFSC, 2013). $B_{msy}$ was set to half of the carrying capacity established by the biomass of the virgin stock after 100 years without fishing. The ABC biomass (*ABCbio* = allowable biological catch), which is the allowed annual fishing quota for the next year, is calculated using the following rules:

The annual quota biomass is converted to bushels of clams and is capped by an imposed total allowable catch, which in these simulations is 3.5 million bushels. This cap is established by the fishery management plan (FMP) (MAFMC, 1986).

**Simulations**

Simulations were performed to compare a series of behavioral choices available to the captains, identified through interviews with industry representatives and captains. These choices include (a) the degree to which captains rely on recent catch history to determine where to fish, (b) whether a captain undertakes searching behavior to determine where to fish, (c) the degree to which captains communicate with each other about their catches, (d) the skill of the captain while fishing, and (e) the degree to which captains avail themselves of federal survey data. Although illegal harvesting is often a component of behavioral choice (*e.g.*, McCay, 1984; Haring and Maguire, 2008; Bashore *et al*., 2012), the requirement that each cage of surfclams receive a tag prior to off-loading has eliminated illegal fishing from the surfclam industry; thus illegal harvesting was not included in this study as an option.

We compared two vessel sizes, small and large, and four ports that encompass most of the primary homeports as they have existed over much of the history of the industry. We included two domains, one typical of the 1980s-mid-1990s prior to the most recent phase of warming of the Mid-Atlantic Bight, wherein surfclams extended in plentitude to the Chesapeake Bay mouth, and one typical of the 2000s, post-warming, wherein the surfclam range was compressed northward as a consequence of the demise of surfclams inshore from the Delmarva Peninsula to north of Delaware Bay (Fig. 2). During this time, the southernmost ports used in the simulations became uneconomic and thus we include in the post-warming domain ports that are no longer functioning for the surfclam fishery.

We ran 51-year simulations and used the last 25 years to remove the effect of initialization of the captain's memory log in year 1 and to permit the stock to be fished down below virgin stock size. Analysis of simulation results focused on the following metrics: the time spent fishing,

$$if\ Fbio > 0.5\,B_{msy} \quad then \quad ABCbio = 0.75\,Fbio\left(1 - e^{-F_{msy}}\right); \quad (3)$$

$$if\ Fbio < 0.25\,B_{msy} \quad then \quad ABCbio = 0; \quad (4)$$

$$otherwise \quad ABCbio = 0.75\,Fbio\left(1 - e^{\left(-F_{msy}\,\frac{Fbio}{0.5\,Bmsy}\right)}\right). \quad (5)$$

the differential in catch between that anticipated if all trips returned to port fully loaded and the landed catch, the distance traveled by the boat to the fishing ground, LPUE (calculated as $\frac{landings}{total\,on-bottom\,time}$), the number of 10-minute squares fished per year, and the net revenue for the vessel. Net revenue is calculated relative to a stipulated ex-vessel value of the catch and the cost of fuel; accordingly, relative variations in net revenue are more important than the actual value. We did not vary the biological processes determining stock performance and distribution during a simulation. Stock biomass was set to approximate the density of clams observed by the federal survey (NEFSC, 2013). As a consequence, the biological reference points did not affect the outcome as the ABC always exceeded the FMP cap. Thus, the quota was invariant over the 51-simulated years. This is precisely the case for the surfclam fishery for most of the 2000s (NEFSC, 2013).

## Results

Certain outcomes of the model depend on the choice of random numbers, particularly the distribution of recruits among 10-minute squares. Consequently, a series of simulations was conducted to evaluate the influence of random number on simulation outcome (Fig. 4). This analysis showed that the choice of seed number for the random number generator did not substantively affect the economics of the vessel, LPUE, hours spent fishing, average distance traveled from the port to the fishing ground, or the degree to which the vessel returned to port fully loaded. Thus, results presented subsequently are limited to single simulations for each combination of decade (1990s versus 2000s), vessel size (small versus large), and captain's behavioral choice.

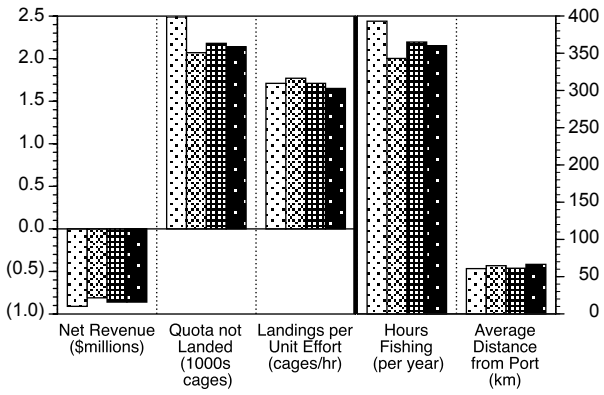


Fig. 4. Results of four simulations in which the seed number for the random number generator was varied. The left three variables are quantified using the left y-axis labels. The right two variables are quantified using the right y-axis labels.

The yearly quota is ultimately distributed to each boat in proportion to its hold capacity. Vessels can take up to two trips per week, but the available quota does not permit two trips per week for each week of the year. Poor fishing performance limits the success of trips and this is measured by the differential between the catch landed and that which could be landed if the boat arrived at the dock full. Simulations showed that small boats normally caught most of their yearly quota allocation (Fig. 5). Large boats performed distinctly more poorly. Boats fishing out of Port 1, the southernmost port, failed to catch their quota allocation to a much greater extent than boats fishing out of the other 3 ports (Fig. 5). That is, vessels fishing out of Port 1 often returned to the dock only partially full. With rare exceptions, vessels fishing at consecutively more northerly ports showed improved performance relative to the neighboring port to the south. Both of these outcomes are anticipated by the contraction of the surfclam's range at its southern and inshore boundaries that increases the time steaming to the more distant fishing grounds in the south and thus reduces the time spent fishing during the trip.

The behavioral choices available to the captains introduced clear differences in performance (Fig. 6). Simulations showed that captains that searched frequently (bold captains) performed less well than the standard

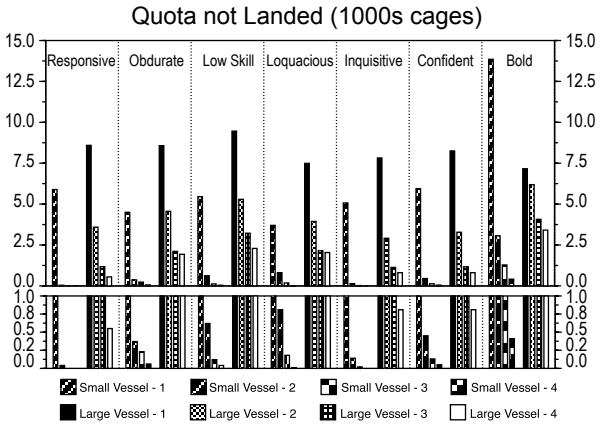


Fig. 5. The cumulative amount of weekly quota allotment failing to be landed each year (in thousands of cages where 1 cage = 32 bushels and 1 bushel = 53 L) for the fleet fishing during the 2000s from each of the four ports with each of two vessel sizes. Note that higher bar values indicate poorer fishery performance in that less of the allocated quota was landed. Boats were allotted enough quota each week to permit one or two full trips. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Lower graph magnifies the y-axis scale from 0 to 1 to render visible the performance of ports 3 and 4. Captain attributes are summarized in Table 2.

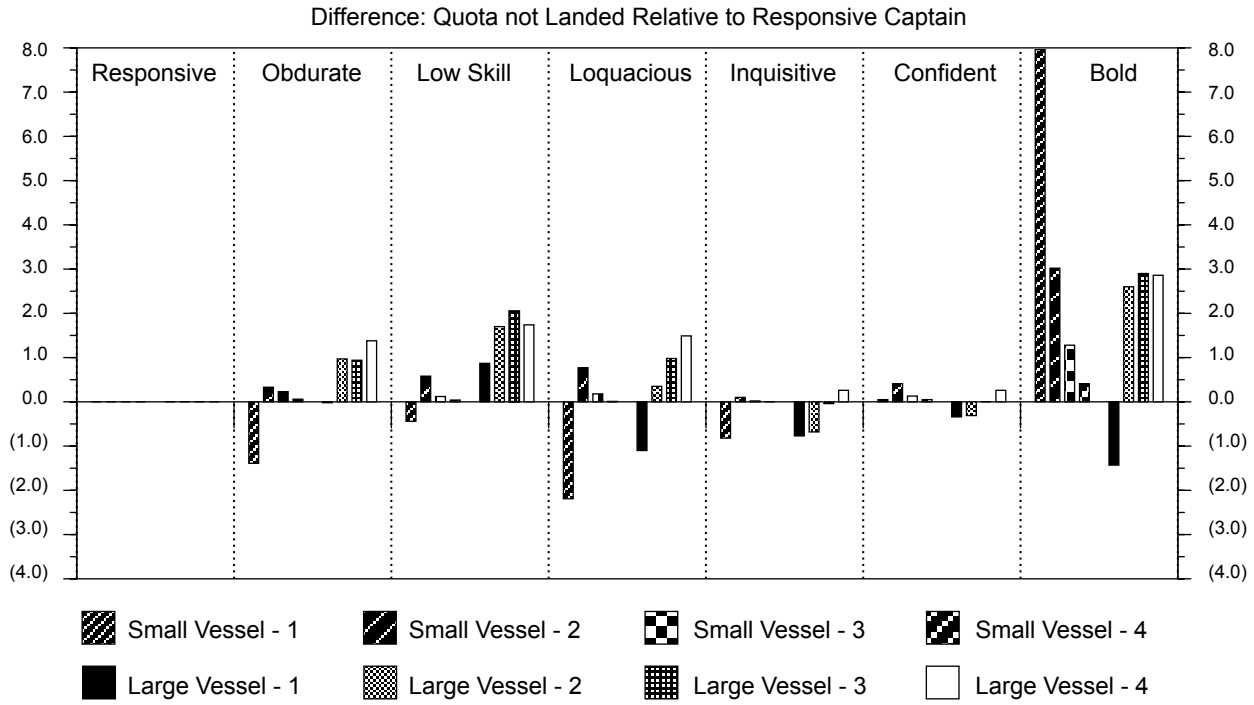


Fig. 6. The cumulative amount of weekly quota allotment failing to be landed each year (in thousands of cages where 1 cage = 32 bushels and 1 bushel = 53 L) for the 2000s fleet fishing from each of the four ports with each of two vessel sizes relative to the amount of weekly quota allotment remaining unlanded by the responsive captain from that port skippering that vessel size. Boats were allotted enough quota each week to permit one or two full trips. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Note that the responsive captain is compared to himself; thus the difference is zero. Positive differences show cases where the value for the responsive captain was lower; that is, cases where the responsive captain landed more of the allotted quota and thus had less unlanded quota. Captain attributes are summarized in Table 2.

(timid) captains with the exception of skippers of large vessels from Port 1 where bold captains performed better. Captains that fished with lesser skill performed poorly relative to the standard (skilled) captain. Those that used a longer period of past performance (obdurate captains) to choose fishing locations and those that communicated (loquacious captains) tended to perform less well than captains that used survey data (inquisitive captains) or occasionally searched (confident captains), but this trend was primarily a feature of large vessels fishing from northern ports (Fig. 6).

More of the allocated quota was caught under 1990s compared to 2000s conditions for nearly all vessel-port combinations (Fig. 7). Simulations indicated that differences were greatest at southern ports where vessels underperformed to a much larger degree under present-day conditions in comparison to the past. Captains that searched and responsive captains, those that made fishing decisions based on the most recent catch record, were most penalized if fishing out of Ports 1 or 2. Captains of large vessels that based fishing decisions on a longer term remembrance of past performance were also penalized if fishing from Ports 1 or 2. Overall, however, the behavior of captains little influenced the degree of difference between past and present-day performance. Changes in the distribution of the stock relative to the vessels' homeports and vessel characteristics dominated the outcome.

Simulations showed that large vessels were more profitable than small vessels under present-day conditions (Fig. 8). Simulations of small vessels often indicated that these vessels were not being operated at a profit. This is consistent with interviews of participants in the industry that reported that vessel operations were frequently subsidized in some measure by the processing plants for which they fish. Nevertheless, economic information for these vessels is sufficiently uncertain in terms of fuel prices, clam prices, and maintenance costs that the following economic analyses focus on the differential in revenue between simulated cases rather than the absolute values.

Simulated vessels fishing from more northerly ports were more profitable than those with southern homeports. Profitability increased modestly if captains communicated

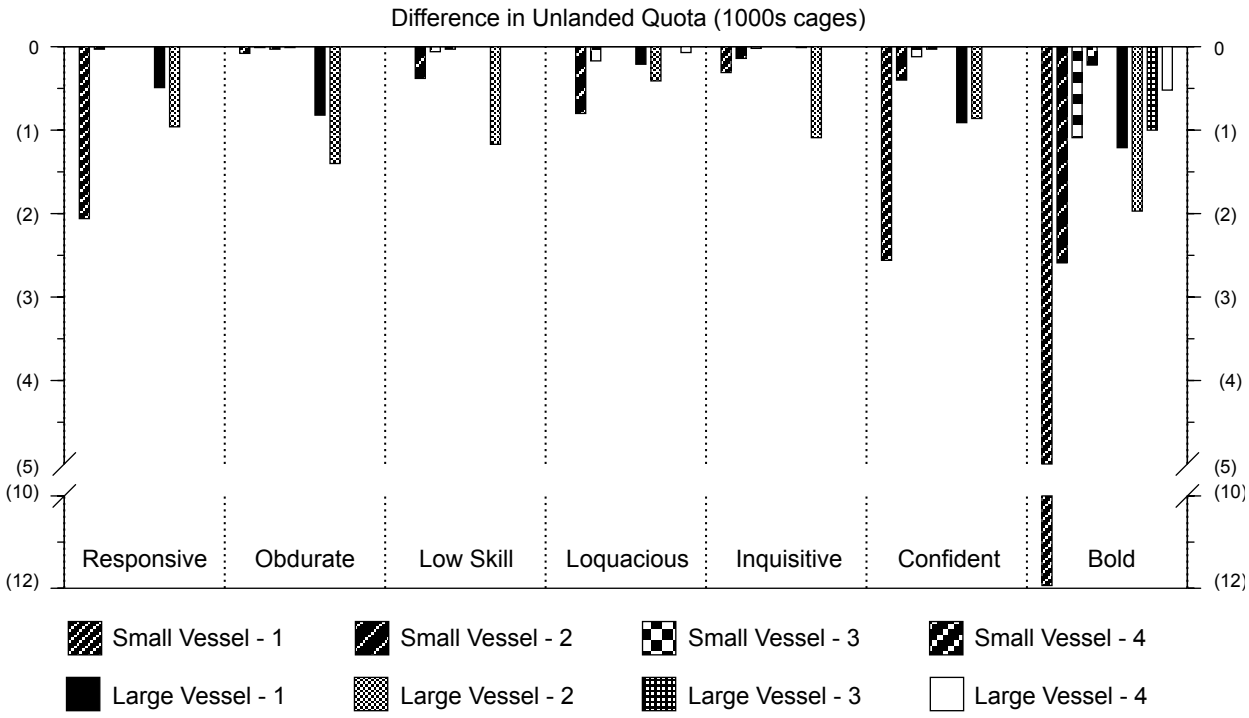


Fig. 7. The difference between past and present performance as measured by the differential in the amount of weekly quota allotment unlanded each year (in thousands of cages where 1 cage = 32 bushels and 1 bushel = 53 L) for the fleet fishing from each of the four ports with each of two vessel sizes. Boats were allotted enough quota each week to permit one or two full trips. A negative value indicates less unlanded quota (better fishery performance) during the 1990s compared to the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

(loquacious), used survey data (inquisitive), or occasionally searched (confident) (Fig. 9). Profitability decreased with low skill and with frequent searching (bold captains). Profitability was higher for all boat-port combinations under past conditions. Stock contraction was the dominant arbiter in the comparison of net revenues between past and present day. Greatest changes occurred for vessels fishing out of Port 1 and a south to north trend was frequently present, such that the differential between past and present day was less at more northerly ports, consistent with the greatest changes in stock distribution being farther south. The behavior of captains did not noticeably affect the outcome.

Simulated LPUE averaged about 1.5 to 2 cages per hour on small boats except for Port 1 where values nearer one were obtained regardless of captain under present-day conditions (Fig. 10). Simulated LPUE on large boats averaged around 3 to 4 cages per hour regardless of port, again with the exception of Port 1 (Fig. 10). Captains with low skill and obdurate captains, those using a longer record of performance to choose a fishing location, underperformed, as did loquacious and bold captains, particularly those fishing from more northerly ports (Fig. 11). Use of survey data improved performance modestly for captains fishing out of Port 1 (Fig. 11). Occasional searching (confident captain) offered little benefit. LPUE did not vary consistently between past conditions relative to present day (Fig. 12). LPUE for large vessels tended to be higher under present-day conditions at more northerly ports. LPUE for captains that searched declined in the 2000s in most cases, whereas the outcome for other behavioral choices was port and vessel specific without consistent trend.

Simulations under present-day conditions showed that large boats fished farther from their homeport on the average (Fig. 13). Thus, total distance traveled per year averaged higher for large vessels than small vessels. This is consistent with the higher steaming speed for large vessels. Vessels fishing out of Port 1 traveled much farther than vessels fishing out of other ports. Often, but not always, vessels fishing from the two most northerly ports traveled a lesser distance than vessels fishing from Port 2. The distance traveled decreased if captains communicated or used survey data, but only if fishing from the three more northerly ports (Fig. 14). Behavioral choice little influenced distance traveled when fishing out

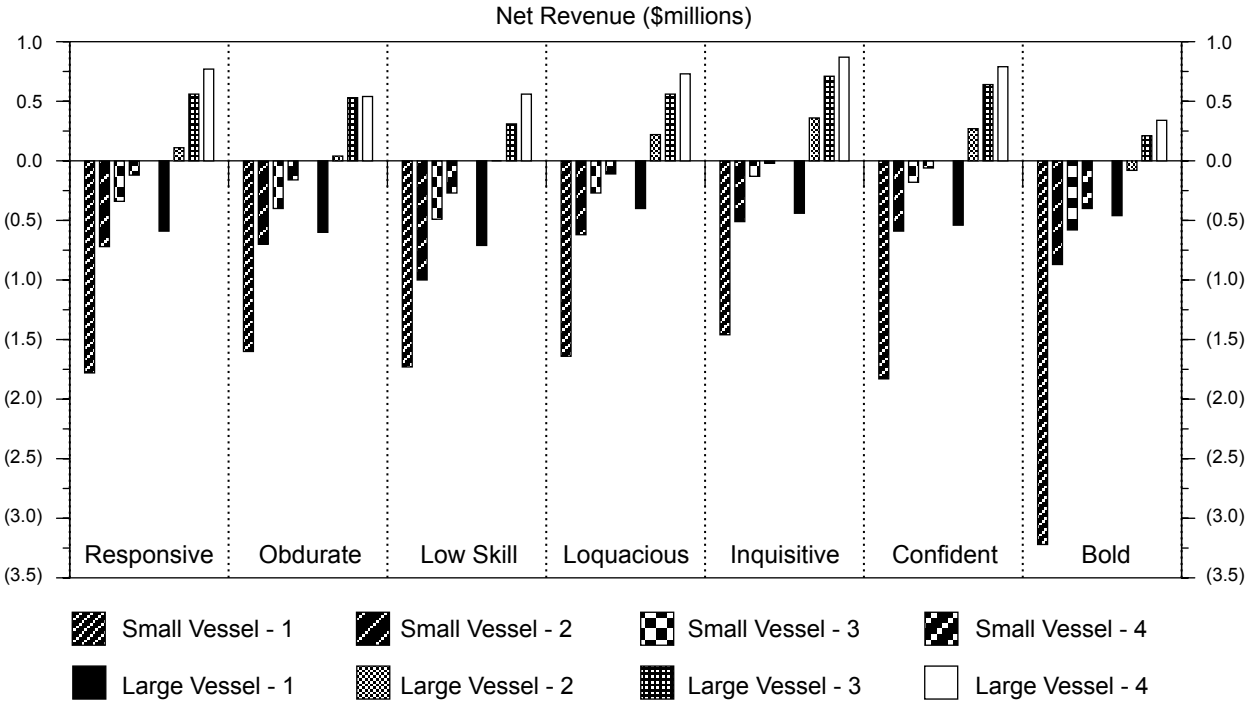


Fig. 8. The yearly net revenue (in millions of dollars) for the 2000s fleet fishing from each of the four ports with each of two vessel sizes. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

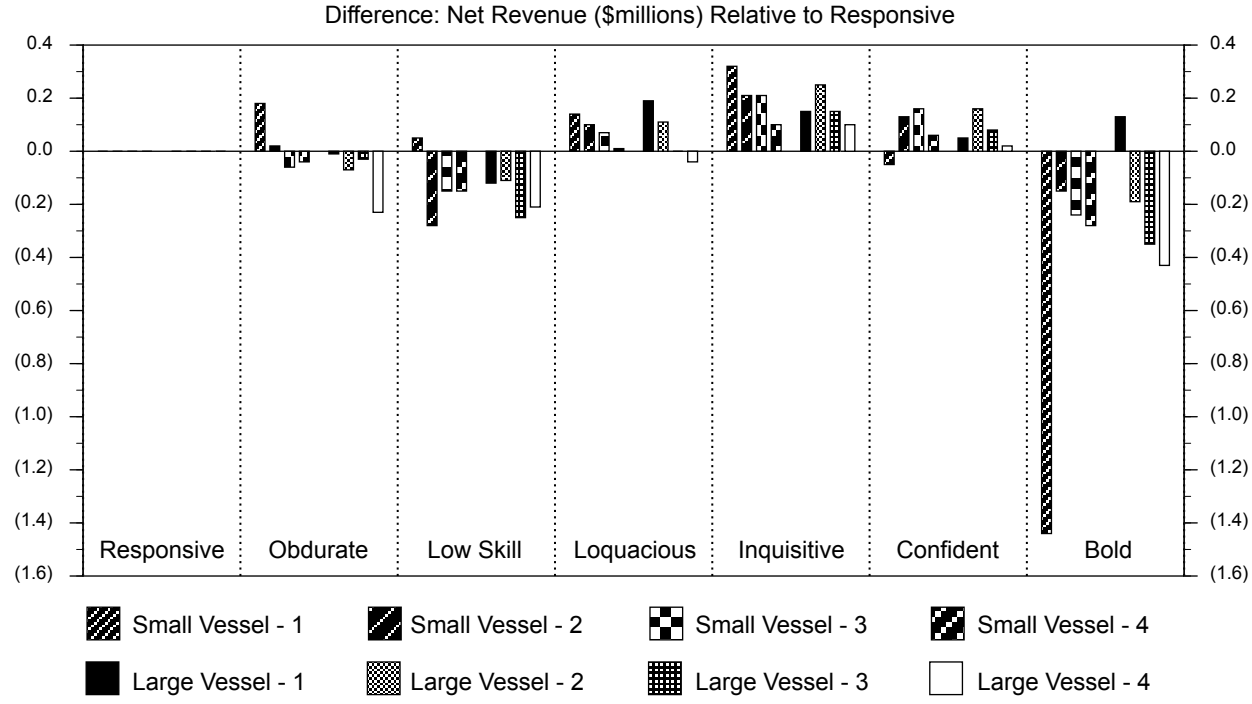


Fig. 9. The yearly net revenue (in millions of dollars) for the 2000s fleet fishing from each of the four ports with each of two vessel sizes relative to the yearly net revenue recorded for the responsive captain from that port skippering that vessel size. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1-4, left; large vessel ports 1-4, right. Note that the responsive captain is compared to himself; thus the difference is zero. Positive differences show cases where the value for the responsive captain was lower. Captain attributes are summarized in Table 2.

of Port 1, except if the captains of large vessels searched. Searching reduced travel time from Port 2, but increased travel time in most cases. Reduced distance traveled did not necessarily improve vessel economics. For example, distance traveled declined for the loquacious captain, but so did LPUE, so that net revenue was only modestly affected. The distance between port and fishing ground increased under present-day conditions compared to the past for most port-vessel combinations. Largest differences were at Port 1; smallest at Ports 3 or 4. Searchers (confident and bold captains) were least affected overall, as these captains tended to steam farther from port regardless of stock distribution (Fig. 15). Captains with low skill or who based fishing decisions solely on catch history (responsive and obdurate captains) were impacted more than loquacious captains or captains that used survey data (inquisitive captains). Thus, responsive captains, those who based fishing decisions on recent catch history, tended to travel less far from port in the past than present day relative to captains that searched. Captains that used the survey or that communicated tended to travel less far from port in the past than present day relative to responsive captains (compare Figs. 14 and 16).

Large vessels spent more time fishing than small vessels, consistent with their larger hold capacity, the differential effect on vessel economics being mitigated by their higher LPUE. Differential in time at sea was primarily a function of the choice of fishing location, not time spent fishing. Effort typically increased to the south with vessels from Port 1 exerting substantially more effort than vessels from other ports (Fig. 17); this consequently lowered LPUE (Fig. 10). The behavior of captains influenced effort. For captains of low skill, captains that employed a longer-term remembrance of past fishing activities in determining locations to fish (obdurate captains), and bold captains, those that frequently searched, effort increased relative to the standard (responsive, skilled, timid) captain (Fig. 18) at most ports. The singular exception was the influence of behavior for large vessels fishing out of Port 1. Here, effort decreased relative to the standard captain for loquacious captains, captains that used survey data (inquisitive), and captains that searched. These vessels traded increased steaming time to fish where LPUE was higher, thereby reducing fishing effort. Hours fished increased in some cases and decreased in others under present-day conditions in comparison to the past (Fig. 19). This conforms with the highly port-specific and vessel-specific effects on LPUE imposed by a contraction in the surfclam's range. The differential tended to be greatest for Port 1 where effort was higher in the past due to the much greater time spent steaming under present-day conditions. Effort increased with frequent searching under present-day conditions, but LPUE was higher in the past, which explains the increased

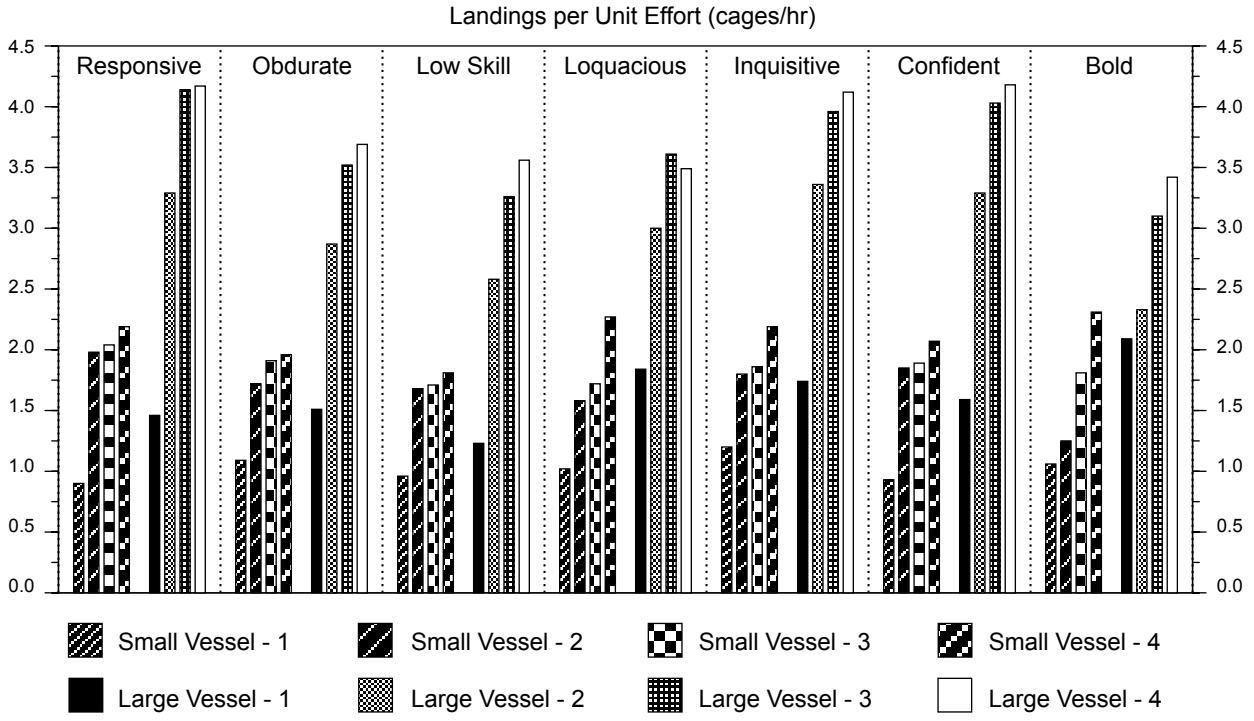


Fig. 10. Landings per unit effort (LPUE in cages hr-1) for the 2000s fleet fishing from each of the four ports with each of two vessel sizes. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

tendency for vessels fishing out of Port 1 to return to port without a full load under present-day conditions. Thus, frequent searching from southern ports was less beneficial as range contraction occurred.

Simulations under present-day conditions showed that most vessels fished on fewer than 10 10-minute squares per year regardless of vessel size or port (Fig. 20). Bold and confident captains visited significantly more 10-minute squares, consistent with their searching behavior. Bold captains visited more 10-minute squares than confident captains in keeping with their higher searching frequency, but not proportionately, as just so many squares could be reached by these vessels in the allotted time at sea. Thus bold captains often revisited 10-minute squares, whereas confident captains did not. The effect was most pronounced for small vessels that were more limited in their searchable region due to their slower steaming speeds. Captains that used survey data (inquisitive captains) also visited an increased number of 10-minute squares. Fewer 10-minute squares were visited by vessels fishing from Port 1. The number of 10-minute squares fished in a given year changed little in the present day relative to the past; however, decreases occurred for captains that searched from southern homeports, Ports 1 and 2 (Fig. 21). This is consistent with the fewer 10-minute squares available to the fishery during present-day conditions for vessels sailing from southern ports.

## Discussion

### Perspective

Surfclams are relatively long-lived relatively immobile animals (Alexander *et al.*, 1993; Weinberg, 1999). Their distribution is dramatically patchy on the scale of 10-minute squares (*e.g.*, Weinberg *et al.*, 2005). These two characteristics generate the most noticeable pattern in the spatial and temporal distribution of effort in the fishery. Vessels tend to return routinely to the same few 10-minute squares and thus a small area of the stock's range supports the majority of the fishery (*e.g.*, NEFSC, 2013; see *e.g.*, Mahévas *et al.*, 2008 for another example of repeated fishing in constricted locations). Because the quota is set well below the allowable biological catch (ABC) by the fishery management plan, the fishery imposes a low fishing mortality rate on the stock; ergo, variations in fishing performance occur slowly because 10-minute squares

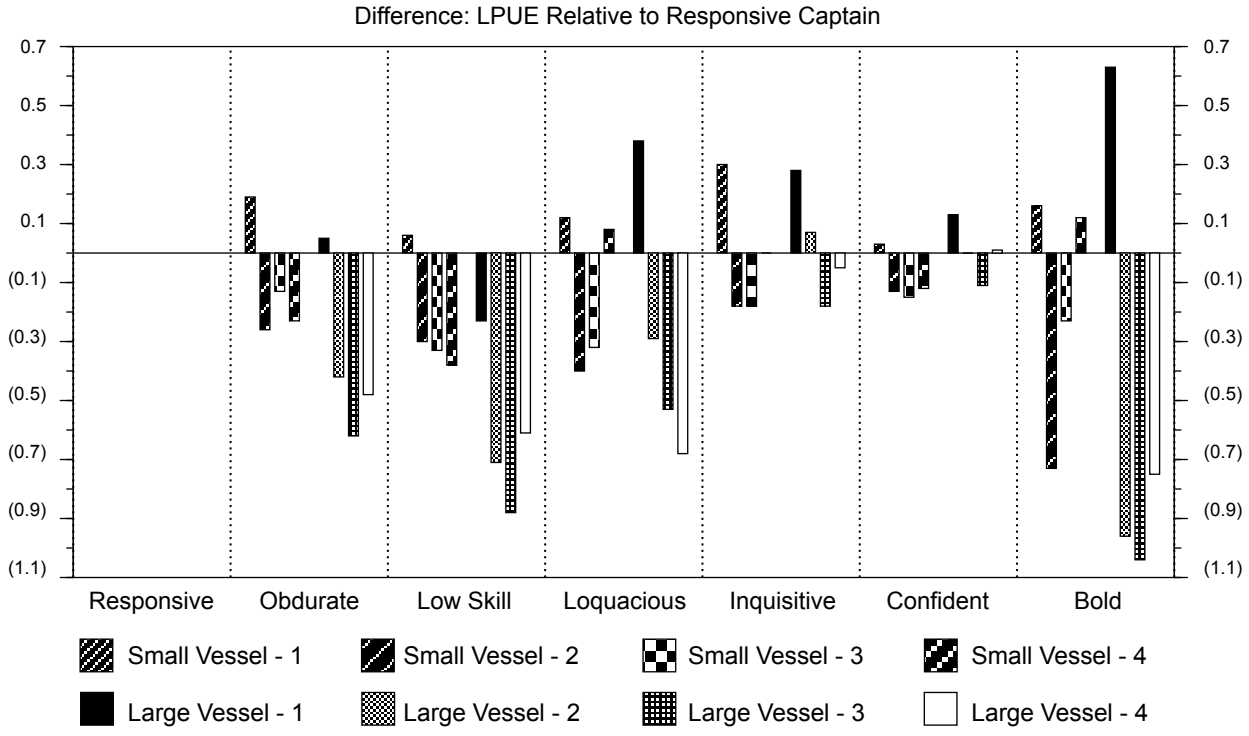


Fig. 11. Landings per unit effort (LPUE in cages hr-1) for the 2000s fleet fishing from each of the four ports with each of two vessel sizes relative to LPUE obtained by the responsive captain from that port skippering that vessel size. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Note that the responsive captain is compared to himself; thus the difference is zero. Positive differences show cases where the value for the responsive captain was lower. Captain attributes are summarized in Table 2.

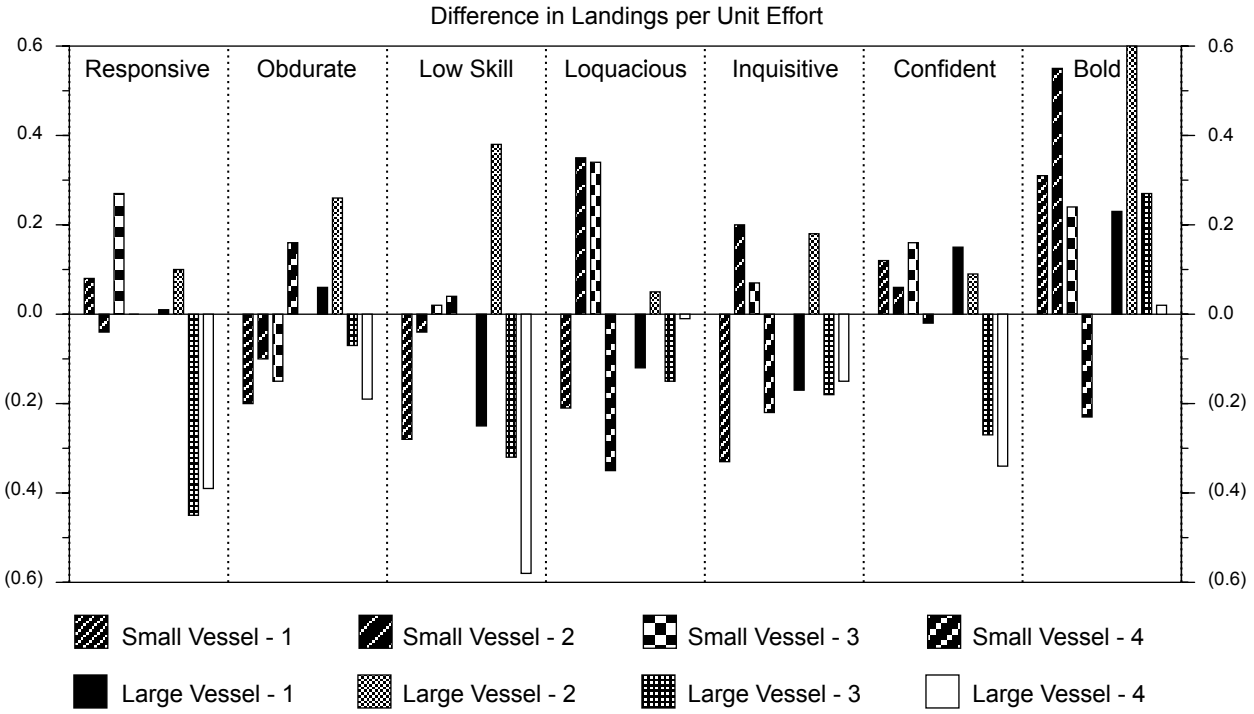


Fig. 12. The difference between past and present performance as measured by landings per unit effort (LPUE) for the fleet fishing from each of the four ports with each of two vessel sizes. A negative value indicates a lower LPUE during the 1990s compared to the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

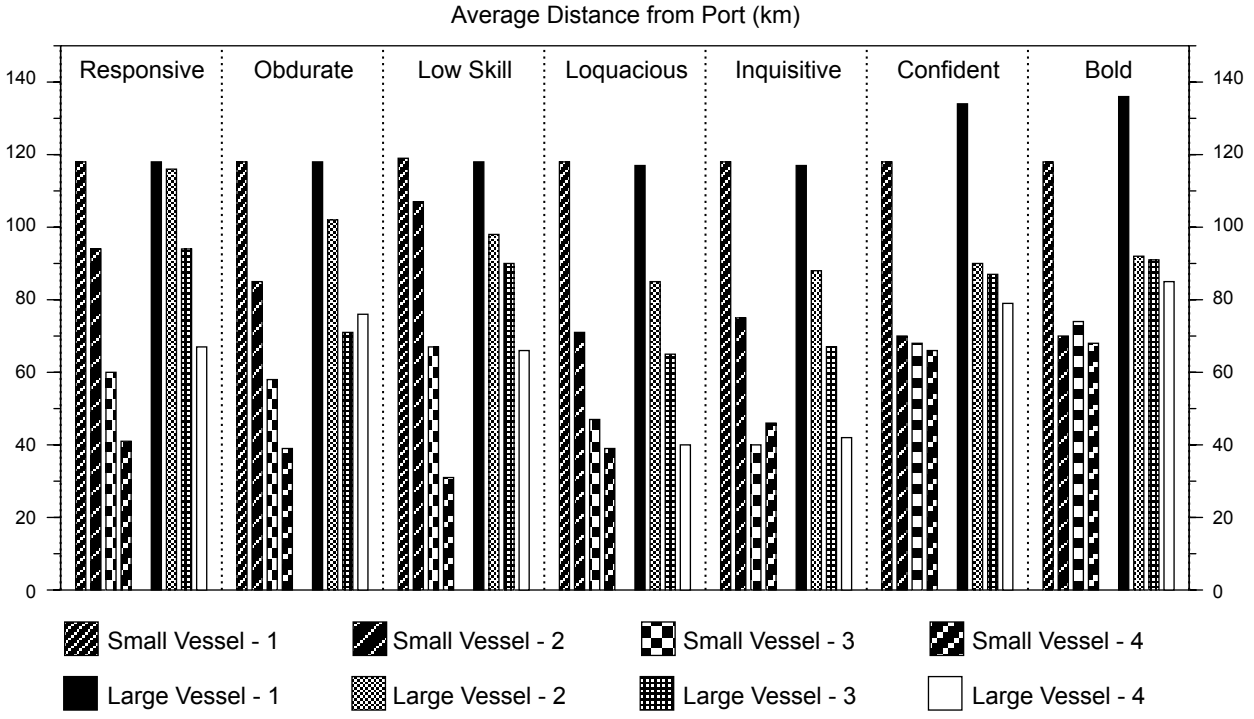


Fig. 13. Average distance traveled from port to fishing ground (in km) for the 2000s fleet fishing from each of the four ports with each of two vessel sizes. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

are fished down over a relatively long period of time. The model reproduces this behavior precisely based on a biological stipulation that the clam is patchy on the scale of 10-minute squares and the premise that captains choose locations to fish that minimize time at sea while permitting the landing of a full vessel load. Thus, determination of the fishing ground for the next trip is based on known catch history and steaming time from port. Here, we examine the influence of a change in stock distribution and a range of behavioral modifications available to the captains that might modify this standard operating procedure.

Given a vessel of average age and thus maintenance cost, a pre-determined ex-vessel value for a bushel of clams, and assuming unbiased availability of quota across the fleet, a vessel's economic performance is primarily determined by time at sea. As fuel use increases while fishing and as fishing consumes a significant portion of time at sea, minimizing fishing time is as important as minimizing steaming time. Setting aside the seasonal and geographic differences in yield (Loesch and Evans, 1994; Marzec *et al*., 2010; Munroe *et al*., 2013), the fleet performance for vessels sailing from a single port is dominated by the degree to which the quota allocated to that port is caught by the vessels fishing therefrom and the degree to which the net revenue for a vessel must be supported by the plant to maintain a positive cash-flow balance. The surfclam industry is vertically integrated, so that plant and vessel profitability are to a certain extent fungible.

Thus, a number of measures of profitability are investigated here, including the degree to which the weekly quota expected to be landed by the vessel was caught and the net revenue for the vessel, a number of measures of vessel performance, including LPUE and fishing effort, and other aspects of fishing behavior, including the number of 10-minute squares visited yearly and the distance from port to the fishing ground. We examined two time periods, a period prior to the late 1990s when the stock south of Long Island was distributed over a broad area of the inner continental shelf from northern New Jersey to Chesapeake Bay and the present-day distribution which includes the expansion of the population inshore along Long Island and a large recession of the southern stock boundary off Delmarva (Weinberg, 2005; Kim and Powell, 2004). The manifest impact of this shift in distribution on the fishery is the decline of clam processing south of New Jersey, the cessation of fishing first from Port 1 (Norfolk, Virginia),

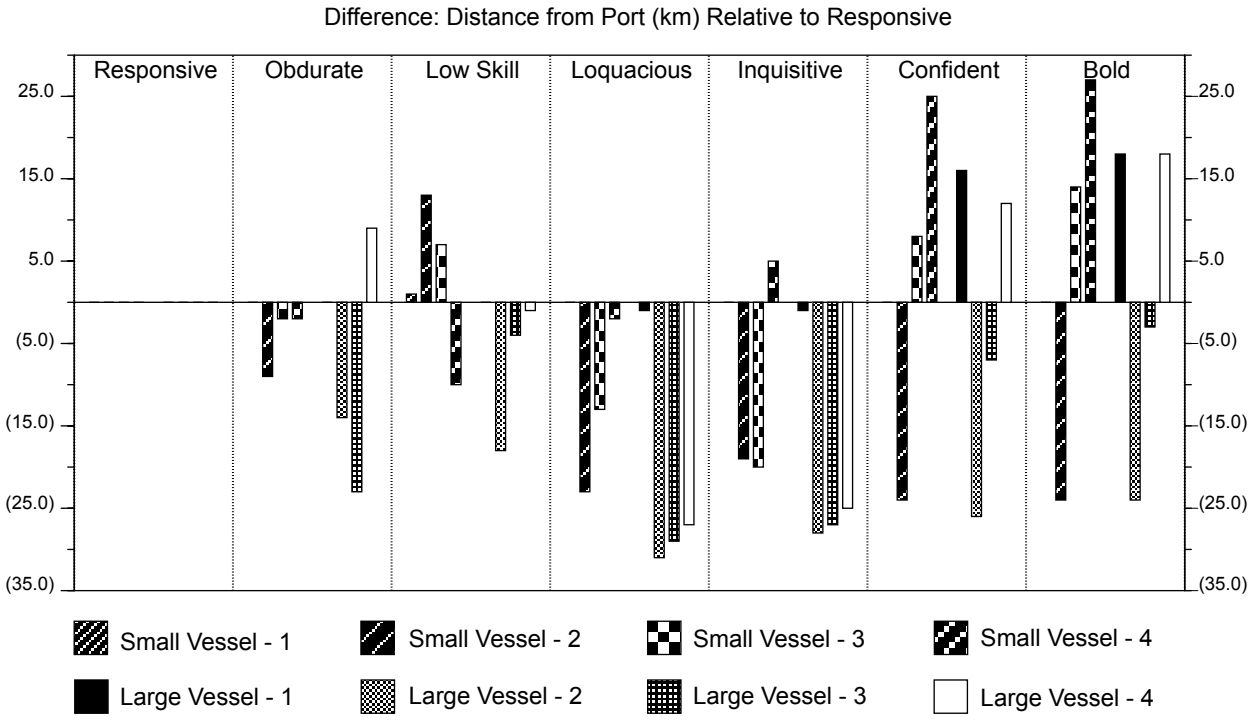


Fig. 14. Average distance traveled from port to fishing ground for the fleet fishing from each of the four ports with each of two vessel sizes relative to the distance traveled by the responsive captain from that port skippering that vessel size, for the case of the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Note that the responsive captain is compared to himself; thus the difference is zero. Positive differences show cases where the val ue for the responsive captain was lower. Captain attributes are summarized in Table 2.

and more recently Port 2 (Ocean City, Maryland), and a decline in landings resulting in an increase in uncaught quota (NEFSC, 2013).

**The influence of stock distribution**

The influence of stock contraction is evinced by a number of metrics in these simulations. In most cases, the differential between the 1990s domain and the 2000s domain occurred throughout the fishery but with a distinctly larger impact farther south. Net revenue declined as vessels steamed farther from port to go fishing and more frequently returned without a full load, although most vessels still returned over 80% full north of Port 1. The differential was dramatically larger for Port 1, the southernmost port, and routinely larger for Port 2 than for Ports 3 and 4. In a few cases, the differential for Port 3 (Atlantic City, New Jersey) was least. Port 3 rests at the latitudinal center of the surfclam's range in the Mid-Atlantic Bight and so is least influenced by shifts at the stock boundaries. Overall, however, net revenue declined between the 1990s and the 2000s, particularly for the southern ports, while changes in LPUE were highly port and vessel specific with little overall pattern, the differential in net revenue being determined primarily by the tradeoff between time fishing and time steaming to 10-minute squares capable of supporting an adequate LPUE. Only the tendency for large vessels to return to port without a full load suggests that large vessels became less economically viable relative to small vessels as a result of stock contraction, but the effect was also restricted to Ports 1 and 2, the southernmost ports. Thus, the differential observed in these simulations was port specific and vessel size-specific.

In the model, large vessels retain a positive revenue stream except at Port 1, whereas small vessels are not profitable at any port. Part of this differential comes from the older age of the smaller vessels that results in higher fixed costs (see model description). Part is due to the lower LPUE. However, simulated small vessels catch their weekly quota allotment more consistently than large vessels and this is not reflected in the vessel net revenue calculation whereas it would be important in the economics of the processing plants: the economics of processing plants are not considered in this study. Thus, the model does not identify an overall bias in performance between the two vessel sizes, although it suggests that continued range contraction may disproportionately impact the larger vessels. Economic and performance data are not available

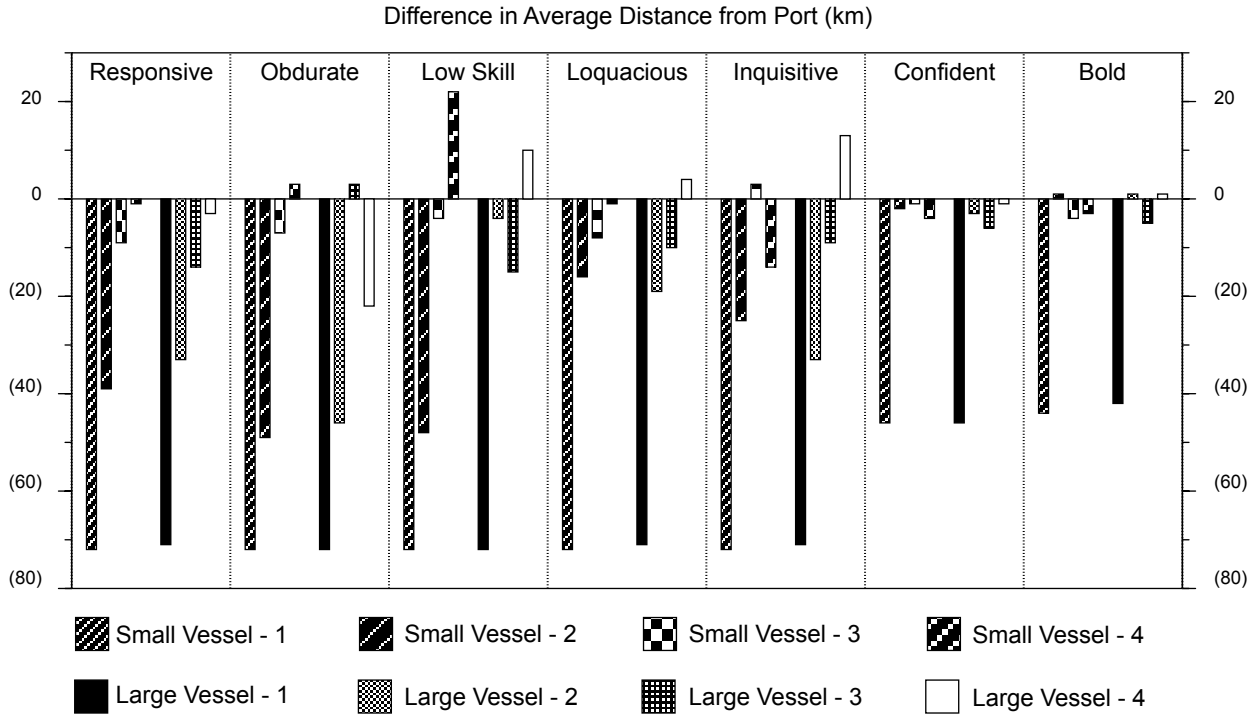


Fig. 15. The difference between past and present performance as measured by the distance between port and fishing ground (in km) for the fleet fishing from each of the four ports with each of two vessel sizes. A negative value indicates a shorter distance traveled during the 1990s compared to the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

to verify many of these conclusions, but the abandonment of Ports 1 and 2 over the last decade is a clear indicator of an overall decline in vessel performance from these ports. This decline is explained in the model by a relative decline in net revenue and an increase in total distance traveled at sea for vessels sailing from these two ports that results in these vessels more frequently failing to catch their weekly quota allotment.

**Behavioral Choice by Captains**

Simulated vessel performance agreed with observations using a few simple rules that relied mostly on recent catch history and the need to limit time at sea. Variations in the behavior of captains under present-day conditions did not much modify the outcome overall. That is, trends in vessel performance based on vessel size and location of homeport were little influenced overall by a range of behavioral modifications diverging from these simple rules.

Reducing skill, thereby increasing effort, reducing LPUE, reducing profitability, and increasing uncaught weekly quota serves to contrast an underperforming captain relative to the responsive captain that fishes according to two simple rules: Rule 1, captains choose locations to fish that minimize time at sea while permitting the landing of a full vessel load; and Rule 2, the information that is used by Rule 1 to determine fishing location is based on the most recent catch history for the vessel. This typical captain is defined as a skilled captain that identifies fishing locations based upon recent catch history (responsive), rarely communicates (taciturn), does not search (timid), and does not use survey data (indifferent). In these simulations, the low-skill captain was specifically defined to perform poorly in comparison to this typical captain.

Some captains may use a longer-term catch history. Obduracy would seem an inappropriate behavior as surfclam densities are unlikely to increase significantly within a previously fished 10-minute square on time periods of one-to-two years and any catch history older than several years is unlikely to provide accurate information as surfclams can grow to market size within 3–4 years (*e.g.*, Munroe *et al*., 2013). Captains no doubt remember locations where submarket clams have been seen and may return to those 10-minute squares some years hence. This behavior was not modeled in this analysis. Here obduracy degrades performance when it

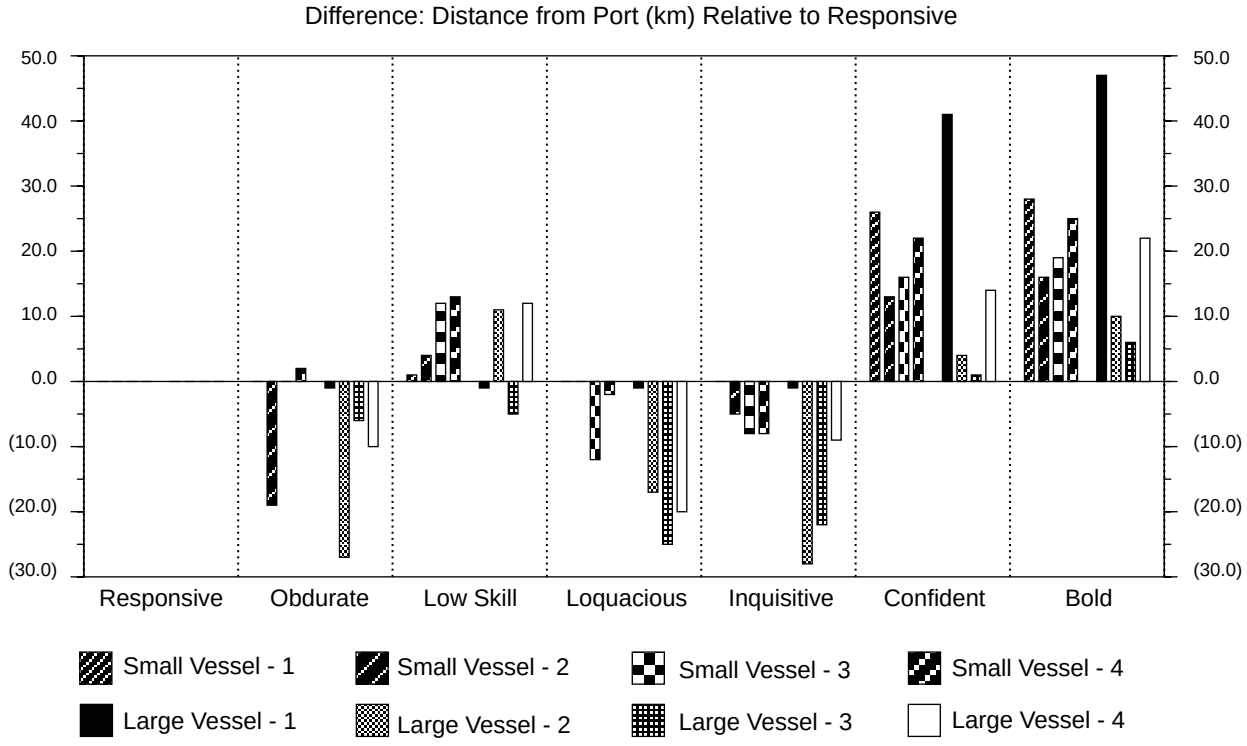


Fig. 16. Average distance traveled from port to fishing ground for the fleet fishing from each of the four ports with each of two vessel sizes relative to the distance traveled by the responsive captain from that port skippering that vessel size, for the case of the 1990s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Note that the responsive captain is compared to himself; thus the difference is zero. Positive differences show cases where the value for the responsive captain was lower. Captain attributes are summarized in Table 2.

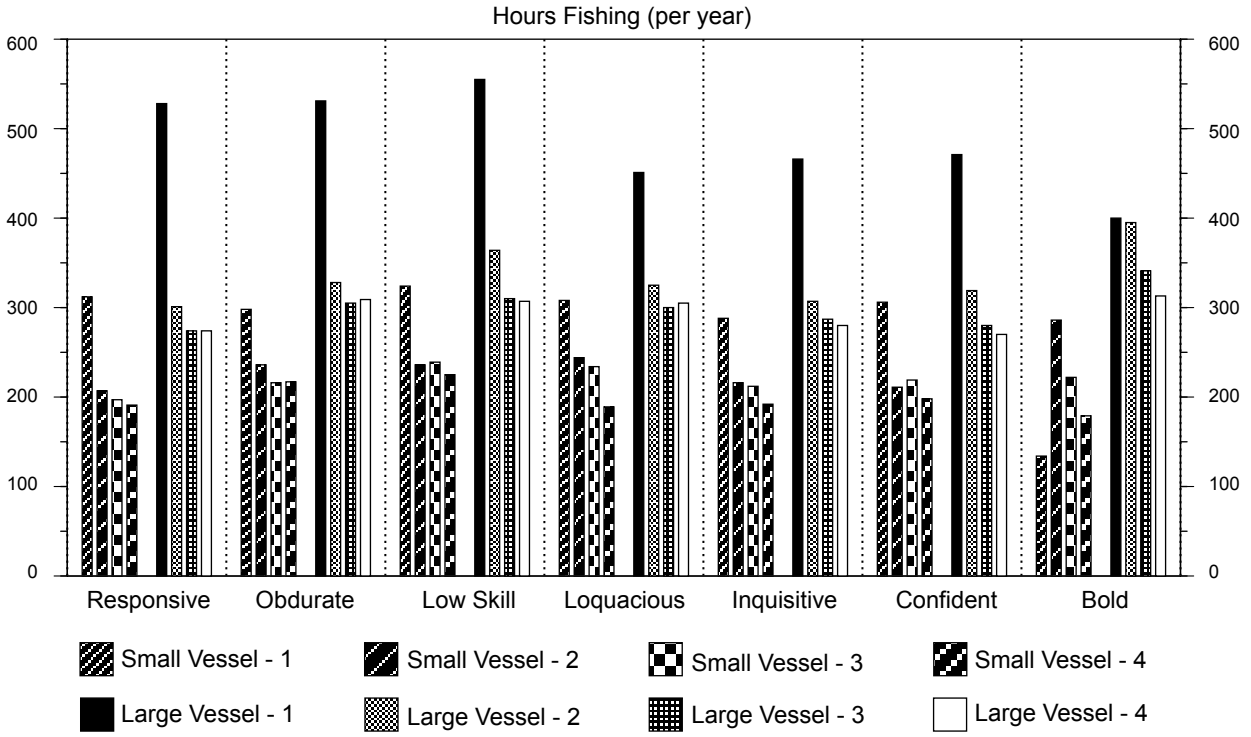


Fig. 17. Average hours fished for the fleet fishing from each of the four ports with each of two vessel sizes, for the case of the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1–4, left; large vessel ports 1–4, right. Captain attributes are summarized in Table 2.

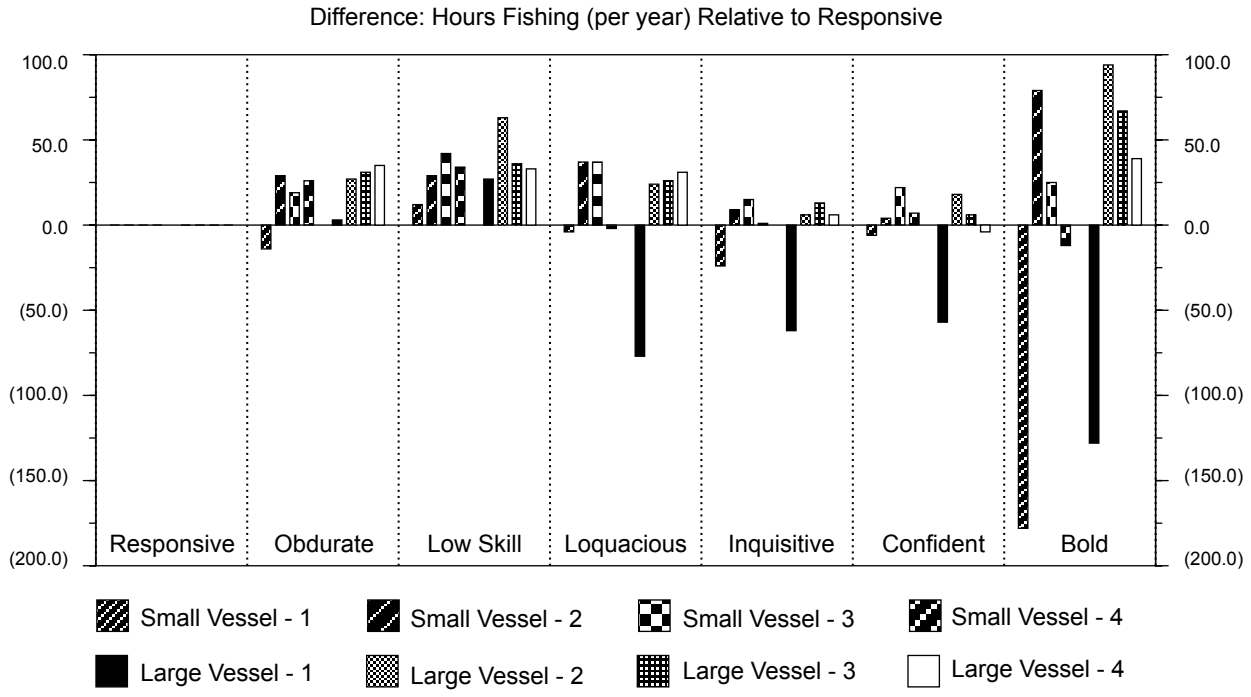


Fig. 18. Average hours fished for the fleet fishing from each of the four ports with each of two vessel sizes relative to the hours fished by the responsive captain from that port skippering that vessel size, for the case of the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1-4, left; large vessel ports 1-4, right. Note that the responsive captain is compared to himself; thus the difference is zero. Positive differences show cases where the value for the responsive captain was lower. Captain attributes are summarized in Table 2.

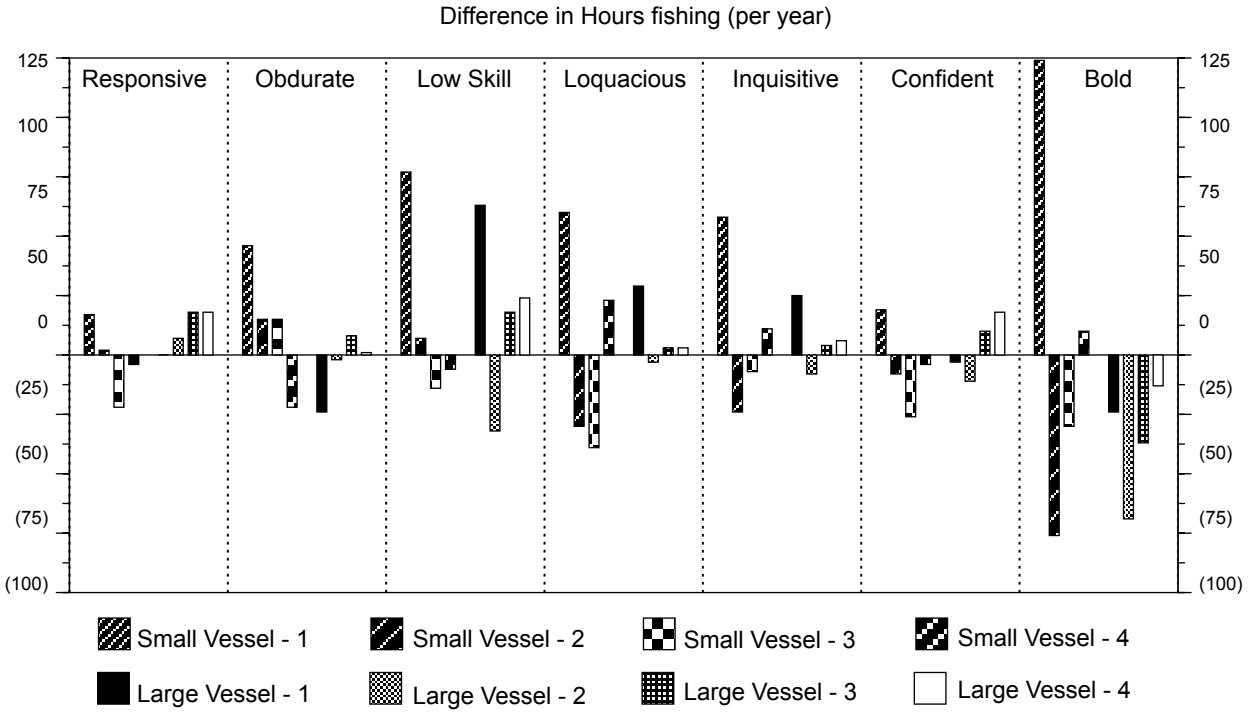


Fig. 19. The difference between past and present performance as measured by the hours fished for the fleet fishing from each of the four ports with each of two vessel sizes. A negative value indicates fewer hours fished during the 1990s compared to the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1-4, left; large vessel ports 1-4, right. Captain attributes are summarized in Table 2.

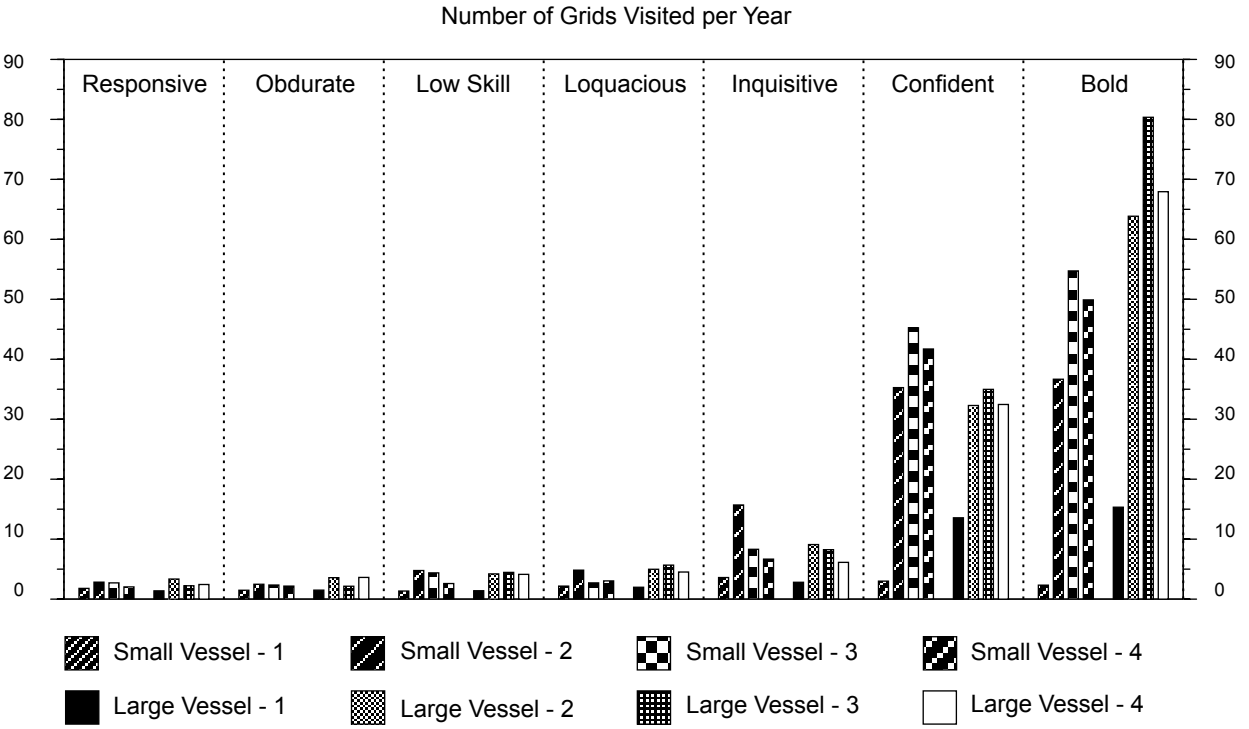


Fig. 20. Average number of 10-minute squares fished for the fleet fishing from each of the four ports with each of two vessel sizes, for the case of the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1-4, left; large vessel ports 1-4, right. Captain attributes are summarized in Table 2.

affects performance at all. Large vessels fail to meet their weekly quota obligations more often, for example, when skippered by obdurate captains (Fig. 6). LPUE is modestly lower for both vessel sizes (Fig. 11). Simulations reinforce the value of returning repeatedly to a few 10-minute squares, a behavior that can be inferred to be advantageous from the known record of fishery landings (NEFSC, 2013). Simulations also reinforce the need for captains to obtain information on fishing locations independent of their personal experience.

Captains report a limited degree of communication within the fleet concerning recent catch histories. In these simulations, loquacity modestly improved performance, particularly by reducing distance traveled (Fig. 14), but the effect was sufficiently limited to suggest that the value of communication will not overbalance the natural tendency for captains to compete in performance. Profitability was marginally affected (Fig. 9) giving limited rationale to modify the competitive nature of between-vessel interactions. Thus, model and observation agree that communication between captains normally is not sufficiently valuable in improving fishing performance to counterweigh the propensity of captains to keep their fishing strategies secret. These results for a fishery on sessile molluscs contrast to a finfish fishery described by Holland and Sutinen (2000) where communication was important due to the mobility of the species.

Searching occurs in most fisheries; however, the success of searching behavior is highly variable (*e.g.*, Dorn, 2001; Powell *et al*., 2003a,b; Millischer and Gascuel, 2006; Bertrand *et al.*, 2007). Surfclam captains report limited searching behavior, though they also report a desire to search more frequently than vessel owners permit. Simulations provide an explanation for this dichotomy. Simulated bold captains, those captains that search frequently, visit many more 10-minute squares than captains with any other behavior (Fig. 20). However, these captains routinely underperform as measured by a variety of metrics. Less of the weekly quota allotment is landed (Fig. 6) and distance traveled from port to fishing ground increases (Fig. 14). LPUE declines (Fig. 11), as does profitability (Fig. 9). Most 10-minute squares produce less than locations known to support high LPUE, so targeting a random 10-minute square on a given fishing trip is very much more likely to reduce performance on that trip than to increase it. Moreover, the bold captain is

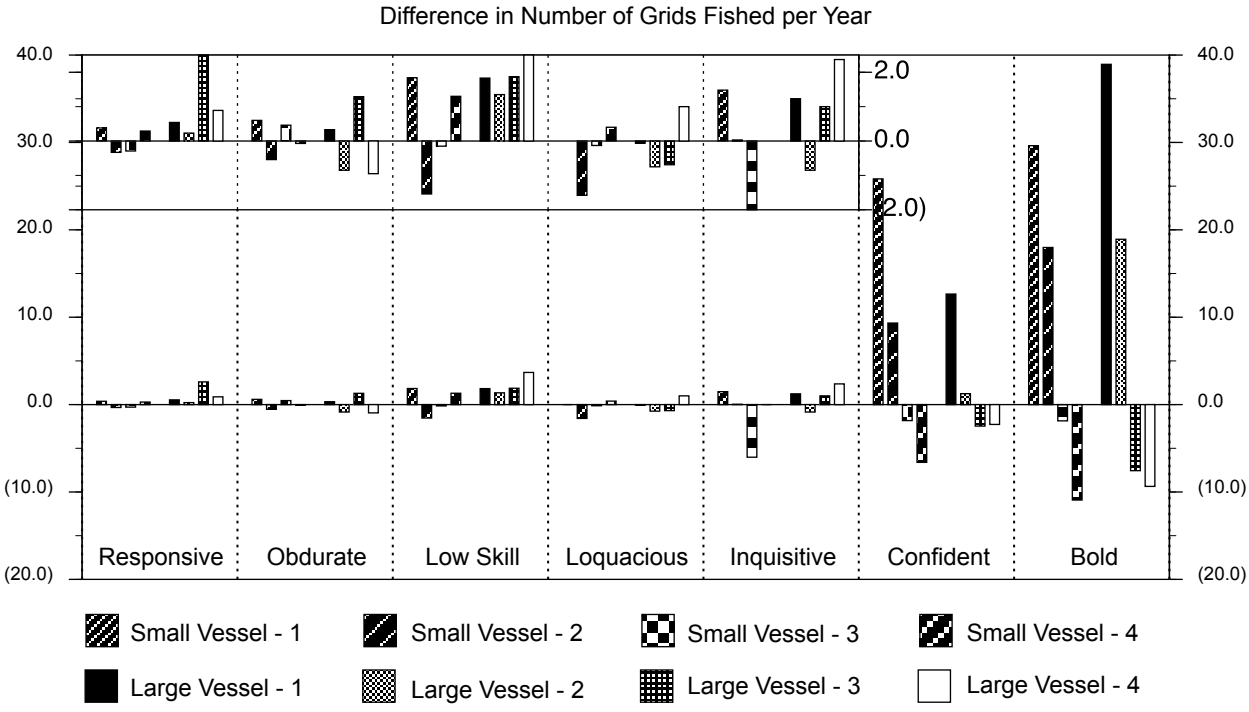


Fig. 21. The difference between past and present performance as measured by the number of 10-minute squares fished for the fleet fishing from each of the four ports with each of two vessel sizes. A negative value indicates fewer 10-minute squares fished during the 1990s compared to the 2000s. Fishing power was maintained equivalent between ports and vessel sizes. Plot is oriented within each group: small vessel ports 1-4, left; large vessel ports 1-4, right. The left five sets of data are shown on an expanded Y-axis scale in the upper left corner with expanded Y-axis values quantified on the (2.0) to 2.0 scale to the right of the insert. Captain attributes are summarized in Table 2.

likely to return to a subpar 10-minute square more than once. Powell *et al*. (2003a,b) and Gillis *et al.* (1993) report other instances where searching lowers LPUE. In contrast, the confident captain searches occasionally. This captain fishes in an increased number of 10-minute squares yearly, but fewer than the bold captain, and rarely returns to an unprofitable square. This captain has modestly increased profitability (Fig. 9) because he remembers and thus returns to the occasionally-found 10-minute square that supports improved LPUE and lesser time at sea. The dichotomy between captains desiring to search and owners limiting requital would appear to stem from an inability to discern the degree of searching leading to a beneficial result relative to its exceedance leading to a disadvantageous outcome.

The surfclam stock is surveyed approximately triennially (NEFSC, 2013). Cruise reports are released to the public soon thereafter (*e.g.*, NEFSC, 1999, 2002). These reports may be valuable in that surfclams, unlike finfish, are immobile at the scale of a 10-minute square and their recruitment and mortality rates auger for considerable stability in market-size abundance over a few years time. Some captains are observed to use these survey reports. Simulations of inquisitive captains showed that survey use improved performance in a number of metrics. The survey reports are, in essence, a free and comprehensive search and the time scale is consistent with surfclam growth rates to market size. That is, one might expect surfclam densities to vary within 10-minute squares on a 3–5 year time span, relatively coherently with the triennial survey.

However, even the greatest differential, the comparison of an unskilled captain with an inquisitive one, shows a limited range in performance. That is, the repertoire of behavioral choices available to captains offers on the one hand only a limited range for improvement in performance, while invoking on the other hand only limited additional risk of deterioration in performance. This outcome is preordained by the sessility of the surfclam and its long life span and low natural mortality rate that foster long-term stability of patches at the 10-minute-square scale of the fishery. Thus, captains need not be imbued with extraordinary sagacity to come close to optimal fishing results, as the implementation of two simple rules, that captains choose locations to fish that minimize time at sea while permitting the landing of a full vessel load and that the information that is used to determine fishing location is based on the most recent catch history for the vessel, are sufficient to achieve near optimal performance.

**Impetus for behavioral adaptation**

Presumably, whatever positive effect behavioral choices may imbue offers increased advantage during times of stock range contraction which reduces the inherent viability of certain homeports and vessel sizes. In fact modeled behavioral choices little influenced the performance metrics between past and present day. Although the fraction of quota uncaught increased from the past to the present day in these simulations, the change was little modulated by the repertoire of options available to the captains (Fig. 7). Variations in behavior varied the average distance traveled from port to fishing ground more in the past (Figs. 14 and 16) probably because a wider range of fishing locations were available prior to range contraction. Captains with low skill performed more poorly under present-day conditions; however, no other behaviors disproportionately impacted performance relative to the standard (responsive) captain under present-day as compared to past conditions, either beneficially or disadvantageously. This study did not investigate cases where surfclam abundance fell sufficiently to force the annual quota below the FMP cap, however, this happenstance has not occurred over the time span of the ITQ fishery (NEFSC, 2013). Thus, certain behaviors may provide increased advantage or disadvantage at lower stock abundances than have been typical over the multidecadal history of the fishery.

**Model Structure**

Fishing vessels are operated by captains that routinely make choices concerning locations to fish. These choices are constrained by vessel characteristics and demands imposed by vessel owners and shore-based dealers. Their aggregate determines performance and performance can vary substantially from vessel to vessel and captain to captain (Dorn, 1998; Gillis *et al*., 1995b; Holland and Sutinen, 2000; Powell *et al.*, 2003a,b; Monroy *et al.*, 2010). The behavior of a fishing fleet and its performance variability has received considerable attention. Models have been constructed in a variety of ways, with individual-based information being implemented in varying degrees (*e.g.*, Bockstael and Opaluch, 1983; Béné, 1996; Holland and Sutinen, 2000; Dorn, 2991; Hutton *et al*., 2004; Mahévas and Pelletier, 2004). In actuality, however, observed dynamics are the sum of trip-wise choices of location and trip-dependent differences in performance and the degree to which longer-term variability in stock dynamics might influence such outcomes may be difficult to extract from models that aggregate information or responses. Here, we have utilized a model that specifies independently each vessel and imbues each captain with specific behavioral proclivities. The model permits captains to respond daily to time-dependent phenomena such as quota allocation and weather. As a consequence, each vessel operates in an inherently independent way and fleet performance is the sum of a set of independent outcomes. As a consequence, this model attempts to reproduce as closely as possible the

individual-based dynamics of a fishing fleet. The model reproduces observed dynamics reported in the literature (*e.g.*, NEFSC, 2003, 2013) and in interview with surfclam captains and industry representatives (see also McCay *et al.*, 2011) and permits investigation of the important components of behavior, vessel characteristic, and surfclam stock dynamic that generate the fleet-wide outcomes obvious in the time series of landings (NEFSC, 2013).

## Conclusions

The response of the surfclam to warming of the Mid-Atlantic Bight is manifested in a substantial contraction of the range generated by the recession of the southern and inshore boundary. This phenomenon has impacted the fishery through the closure of southern ports and the movement of processing capacity north. Potentially, the challenges faced by the fishery require different responses on the part of the vessel captains to mitigate a decline in performance ineluctably accompanying this shift in range. The purpose of this study was to evaluate options in the captain's repertoire that might mitigate the expected decline in performance.

A number of simulated behaviors modestly varied performance. Use of survey data and occasional searching tended to increase performance. Reliance on an older catch history tended to reduce performance as did frequent searching. However, in no case was this differential large and the differential was little modified by a contraction in the surfclam's range. The population dynamics of the clam permit near-optimal performance based on a few simple rules: choose locations to fish that minimize time at sea while permitting the landing of a full vessel load; base this choice on the most recent catch history for the vessel.

A model based on this behavior and the appropriate abundance and patchiness of clams reproduced observed spatial and temporal trends. These included the south-to-north gradient in performance consistent with increased stock abundance north and the tendency for the fishery to repeatedly exploit a limited area of the stock's range over the year (NEFSC, 2003, 2013). Comparison between the 1990s and 2000s demonstrated the increasing marginality of southern ports which is observed in the northward shift in vessel homeports and plant processing capacity. The frequency at which vessels failed to land their weekly quota allotment increased at southern ports and vessel profitability declined due to increased steaming distance to obtain a high LPUE. However, none of these changes compromised the basic approach to fishing observed in the industry and inculcated in the responsive captain used in this study because the underlying variables determining performance beyond port location are determined by the inherent sessility and patchiness of the clam and its long life span which result in temporal variations in patch location and density occurring slowly relative to the decision-making activities and trip frequency of the vessel captains. Accordingly, although captains can avail themselves of a range of approaches to obtain the information underpinning the choice of location for the next fishing trip, these differing approaches impart only modest competitive advantages or disadvantages to the final outcome.

## Acknowledgments

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# Gastric evacuation rates in male Clearnose Skate (*Leucoraja eglanteria*) in the laboratory

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## Abstract

Evacuation rates were determined for Clearnose Skate (*Leucoraja eglanteria*), an important predator in the mid-Atlantic United States shelf ecosystem. Male Skates (570–730 mm total length) were fed Sand Lance *Ammodytes* sp. and allowed to digest from 2–48 hr at two different temperatures. At selected times, fish were removed from tanks, sedated with tricaine methanesulfonate, and subjected to gastric lavage. This procedure was successful at removing the food from the stomachs without injury to the fish. Evacuation rates for the two temperature treatments were fit best by exponential models. The evacuation rates, per hour, were faster at 20°C than at 15°C, resulting in empty stomachs by 24 hr at 20°C, and 48 hr at 15°C. Evacuation rates at these temperatures were estimated as 0.102 and 0.059 proportion stomach contents per hour at 20°C and 15°C. These evacuation rates and their temperature dependence are similar to that of other species of elasmobranchs and some teleosts. Evacuation rates are often combined with stomach content data to estimate consumption. The results of this study indicate that evacuation rates by some skates may be up to five times higher than currently used in multi-species and ecosystem models of the Northeast U.S. Shelf. The implication is that consumption may also be higher, highlighting the need for more research to increase the accuracy in evacuation rates estimates.

*Keywords:* digestion, evacuation, consumption, multispecies modeling, ecosystem modeling, elasmobranchs, skates

## Introduction

The importance of skates in the trophic dynamics of the Northeast U.S. Shelf Ecosystem has been changing. Initially, Link *et al*. (2002) reported that predation by elasmobranchs (1973–1998) had little effect on groundfish numbers or biomass. However, there has been a biomass shift from groundfish to elasmobranchs and crustaceans during the last two decades (Lucey and Nye, 2010), that indicates skates are now among the dominant predators in the shelf ecosystem (Link and Sosebee, 2008; Smith and Link, 2010). Seven species of the family Rajidae are common in the Northeast U.S. continental shelf ecosystem, occupying a variety of depths and temperature ranges (Gabriel, 1992). Clearnose Skates (*Leucoraja eglanteria)* are among the top 50 demersal species by biomass caught on the Northeast Fisheries Science Center (NEFSC) spring and autumn bottom trawl surveys (Lucey and Nye, 2010) but are more common summer residents south of Cape Cod, Massachusetts and are frequently caught in Mid-Atlantic coastal bays (Wilk *et al*., 1998; Packer *et al*., 2003). Large Clearnose Skates (>61 cm; sexes

combined), consume approximately equal proportions of benthic invertebrates, various benthic fishes, and *Loligo* squid (Packer *et al*., 2003; Link and Sosebee, 2008; Smith and Link, 2010). In some areas of the Mid-Atlantic, the proportion of teleosts in the diets of Clearnose Skates approaches 50% (Woodland *et al*., 2011).

To evaluate the importance of Clearnose Skates as predators in the ecosystem, estimates of biomass and consumption rate are needed (see Elliott and Persson, 1978, Durbin *et al*. 1983). Estimates of biomass can be derived from the Northeast Fisheries Science Center bottom trawl survey. Consumption can be estimated from stomach content data and knowledge of the rate at which food passes into the intestine (termed evacuation rate, Bromley, 1994). There is a relatively large amount of stomach contents data from fish in the Northeast U.S. Shelf Ecosystem (Smith and Link, 2010). Food habit information and consumption rates are used in multispecies models and stock assessments to more accurately predict interactions between species such as groundfish and elasmobranchs. Currently, consumption rates are estimated based on information known for other species or regions (Overholtz and Link, 2007) and there is relatively little system-specific information on how rapidly the food is evacuated, or how evacuation rate is affected by temperature. Rate of evacuation and the shape of the evacuation function depend on various factors including temperature, the fish's metabolism, meal size, and the prey's structure, such as soft tissue, exoskeleton, or bone (Fänge and Grove, 1979; Bromley, 1994; Nelson and Ross, 1995).

Our main objective was to determine the evacuation rates of Clearnose Skate, from the Mid-Atlantic region, under controlled laboratory conditions. To measure evacuation rates, we used gastric lavage, which allows one to determine the proportion of stomach contents remaining without sacrificing the fish (Kamler and Pope, 2001; Waters *et al*., 2004; Wanner, 2006). We believe this information, along with that already determined for Little Skate and Winter Skate (Nelson and Ross, 1995; Wunder, 1995), will help provide more accurate consumption information for skates in general and that this information will help improve stock assessments and multispecies models in the region.

## Materials and Methods

Clearnose Skates (570–730 mm total length, 935–1650 g) were collected by otter trawl on three fishing trips 5–10 km off the coast of New Jersey in the last half of August 2013. Water temperature at the nearby Ambrose Buoy averaged 22.3°C over the period of collection (National Climatic Data Center, NOAA). Tow times were <5 minutes, and the captured skates were held in an onboard live-well that received regular changes of seawater. Upon arrival at the dock, the skates were transferred to 64 gallon coolers and transported to the laboratory within 20 minutes. Only male Clearnose Skates were captured.

In the laboratory, skates were maintained in holding tanks (2.5 m diameter; 0.5 m depth) without sediment that received flow-through water from Sandy Hook Bay (salinity 25–26 psu, temperature 20–21°C). The light cycle was maintained at a constant 12 hr light and 12 hr dark. Skates are commonly collected from the Hudson-Raritan estuary at these temperatures and salinities during the late summer (Packer *et al*., 2003). Before experiments commenced, all tanks were gradually decreased in temperature to 20°C ±1.0°C, using a mixture of ambient estuarine water and additions of chilled or heated estuarine water. When experiments at 20°C were completed, all tanks including the holding tanks were gradually decreased to 15°C. Fish were fed a maintenance ration every other day of thawed Sand Lance (*Ammodytes* sp.) or Silverside (*Menidia* sp.) ad libitum. Most skates responded immediately to the presence of food, actively searched the bottom, and consumed the Sand Lances whole. Only fish that ate consistently and showed no external abrasions or injuries were used in experiments. The total number of skates used in experiments was 27.

For each evacuation experiment, eight skates at a time were measured, weighed, tagged, and transferred to individual 1.8 m diameter round tanks. In the first series of experiments, all tanks were maintained at 20°C (±1.0°C), and in the second series, 15°C (±1.0°C). Fish were allowed to reacclimate for one to two days after transfer, and were starved one to two days before each trial. Each skate was then offered four weighed whole Sand Lance, and if those were consumed, another four were weighed and offered. Skates were allowed to feed for 30 min, and then uneaten food was removed, weighed, and subtracted from the amount given. Skates that fed were randomly selected for gastric lavage at different digestion times.

Clearnose Skates that consumed one or more Sand Lances were used for pulsed gastric lavage (Kamler and Pope, 2001). Individual skates were sedated in a cooler containing 20 l of water from their own tanks and 1 g tricaine methanesulfonate. A skate was considered sedated when it could not right itself after being turned over, yet continued to respire. The skate was then removed from the cooler by hand and held ventral side up above a tray, while a hand-pumped compression sprayer nozzle was inserted through the esophagus and into the stomach. A stream of seawater from the sprayer reservoir was gently

and intermittently pumped into the stomach, lavaging the contents out of the stomach. Lavage was stopped when no more visible material from the stomach was seen and the water expelled was clear. The skate was then returned to its tank and allowed to rest for a minimum of two days. Skates that did not eat in the experimental tanks were removed and replaced with other skates from the holding tanks. Skates that did feed were only subjected to four lavages before they were removed from the experimental tanks and returned to the holding tanks. A few skates were dissected after lavage to confirm the efficiency of the procedure.

The evacuate was sieved through 1 mm mesh, drained, scraped onto a damp paper towel, and then weighed (wet weight). Mucous, a product of the digestive system, significantly delayed drainage but error was no more than 0.5 g per stomach, determined by comparison of the weight of an empty wet sieve to the weight of a sieve scraped free of as much mucous as possible.

Evacuation rate, expressed as proportion lost from the stomach per hour, was estimated by statistically modeling percent weight of prey remaining in the stomach by time. Proportion remaining ($W_P$) was calculated by dividing the stomach content weight at the time of sampling ($W_t$) by the total weight of prey presented to each individual. Evacuation rate was then estimated as the loss of proportion stomach weight over time. Many authors conclude that models of evacuation rate with an exponential curve are most apt for carnivorous teleosts, and that linear or square root models are best for elasmobranchs, depending upon prey type (Fänge and Grove, 1979; Durbin *et al*., 1983; Nelson and Ross, 1995). Owing to this uncertainty, we fit both a linear (1) and an exponential (2) model.

$$W_P = W_0 - Rt \quad (1)$$

$$W_P = W_0 e^{-Rt} \quad (2)$$

where $W_P$ is the proportion remaining, $t$ is the time of sampling, $W_0$ is an estimated parameter of the proportion of the meal that enters the stomach, and $R$ is an estimated parameter of the evacuation rate per hour. $W_0$ is often less than 100% owing to the initial expression of liquid from the prey (Olson and Boggs, 1978).

Bromley (1988, 1994) suggested that exponential models of proportion stomach content data are misleading and that evacuation in most species is actually linear. At later hours of digestion, some stomachs with zero contents are found; because proportion stomach content cannot be less than zero these data are in effect censored. To evaluate this assertion we fit equation 1 using linear least square (lm function in *R*) and equation 2 using several statistical fitting procedures: non-linear least squares (nls function in *R*), ln transformed linear least squares (lm function in *R*), a general linear model with Gamma distribution and log link (using the glm function in *R*), and a beta regression with a log link (using the betareg function in *R*) (R CoreTeam, 2014; Cribari-Neto and Zeileis, 2014). These statistical techniques offer a modern approach to that used by Bromley (1988). Models were compared using AIC and $r^2$, but direct comparison of all the models was not possible because of the different transformations and estimation procedures. To avoid errors with log-transforming observations of 0 stomach contents at specific times, it was assumed that 0.01 of the original contents remained.

Evacuation rate decreases with decreasing temperature (Durbin *et al*., 1983) following an exponential model,

$$R = ae^{bT} \quad (3)$$

where $a$ and $b$ are parameters of the exponential model, $T$ is temperature, and $R$ is evacuation rate. This model was fit using the two estimates of evacuation rate at the two temperatures. We recognize that this model was fit with two data points only. Our purpose is simply to estimate the parameters a and b and compare these parameters to other studies that have estimated evacuation rates in skates.

## Results

During the 20°C experiments, gastric lavage was performed 47 times. Randomly selected skates were lavaged at 2, 4, 5, 6, 8, 9, 12, 20 and 24 hrs (Fig. 1A). Skates were observed to eat from 1 to 11 Sand lances during 30 min. Meal sizes ranged from 2.4 to 51.8 g (mean 23.0 g) averaging 1.73% of body weight, (0.20% to 3.2%). Evacuation of the stomachs of Clearnose Skates, or the presence of <5% of the food given, was complete by 24 hr at 20°C (Fig. 1A).

During the 15°C experiments, gastric lavage was performed 28 times. Randomly selected skates were lavaged at 4, 5, 20, 24, 28, and 48 hrs (Fig. 1B). Skates were observed to eat only from one to seven Sand lances during 30 min. Meal sizes ranged from 4.7 to 34.8 g (mean 19.2 g) averaging 1.39% of body weight (0.39% to 3.81%) ($n$ = 28). Complete evacuation of the stomachs, or the presence of <5% of the food given, occurred by 48 hr at 15°C (Fig. 1B). After the lavage procedures, the skates recovered from sedation within 10 or 15 minutes. No observable negative effects were seen from lavage or sedation.

The exponential model (Eq. 2) fit the data better than the linear model (Eq. 1) comparing both AIC and $r^2$ values (Table 1). The various approaches to fit the exponential model all yielded similar results (Table 1, Fig. 2). Based

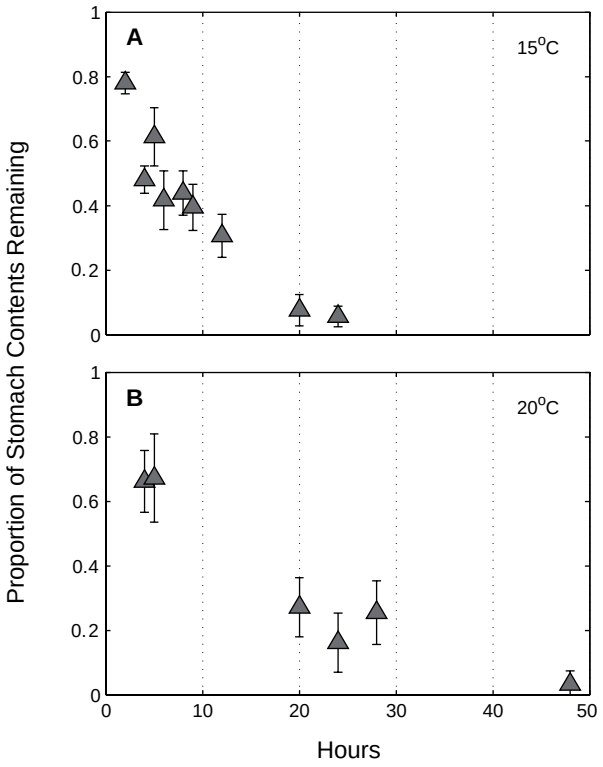


Fig. 1. Mean percent (± 1 standard error) of food digested by hour in Clearnose Skate, *Leucoraja eglanteria*, at **A**) 20ºC and **B**) 15ºC.

on the nonlinear fit of the exponential model, gastric evacuation rates were 0.102 at 20°C and 0.059 at 15°C. The estimates of evacuation rates in this study are comparable with estimates made for other *Leucoraja* species (Table 2 and Fig. 3).

The model of temperature dependence ($R=ae^{bT}$) estimated $a$ = 0.011 and $b$ = 0.109 (Fig. 4). These parameters should be viewed cautiously as only two temperatures were used in their estimation. However, the $b$ term of the temperature dependence model was comparable to estimates for teleosts: Elliott (1972) estimated $b$ = 0.112 and Durbin *et al*. (1983) estimated $b$ = 0.111 (Fig. 4). The $a$ term for Clearnose Skates was lower than that for teleosts: Elliott (1972) estimated $a$ = 0.053 and Durbin *et al*. (1983) estimated $a$ = 0.041. These functions we determined are higher than what is used in many regional multispecies models (*e.g.* Link and Sosebee, 2008) and suggest some phylogenetic concurrence in evacuation rate among skates (Fig. 4).

## Discussion

We found that gastric lavage works well in Clearnose Skates and they are very good laboratory animals. Skates have simple stomachs with an open esophagus and a sphincter at the posterior end, so lavage efficiently washes out the stomach's contents. Wunder (1995) also found that

Table 1. Clearnose Skate, *Leucoraja eglanteria:* Linear and exponential models, Akaike's Information Criterion (AIC) values, and parameter estimates for the best fit models of evacuation rate in the laboratory. $W_0$ is the y intercept, $R$ is evacuation rate, and SE is standard error. Parameter estimates are provided for the best fit model only. $N$ for 20ºC was 47, and for 15ºC, 28.

| Temp. | Model | $r^2$ | AIC | $W_0$ | | R | |
|---|---|---|---|---|---|---|---|
| | | | | Estimate | SE | Estimate | SE |
| 20ºC | Linear (Eq. 1) | 0.69 | -42.6 | 0.698 | 0.036 | -0.029 | 0.003 |
| 20ºC | Exponential (Eq. 2; non-linear fit) | | -49.7 | 0.909 | 6.191 | -0.102 | 0.011 |
| 20ºC | Exponential (log transformed; linear fit) | 0.75 | | 1.263 | 0.181 | -0.164 | 0.014 |
| 20ºC | GLM (Gamma Distribution, link=log) | | | 1.029 | 0.178 | -0.119 | 0.014 |
| 20ºC | Beta (link=log) | 0.75 | | 0.933 | 0.068 | -0.109 | 0.011 |
| 15ºC | Linear (Eq. 1) | 0.75 | -32.9 | 0.634 | 0.045 | -0.014 | 0.002 |
| 15ºC | Exponential (Eq. 2; non-linear fit) | | -49.8 | 0.860 | 0.059 | -0.059 | 0.006 |
| 15ºC | Exponential (log transformed) | 0.77 | | 1.124 | 0.253 | -0.081 | 0.009 |
| 15ºC | GLM (link=log) | | | 1.007 | 0.239 | -0.067 | 0.008 |
| 15ºC | Beta (link=log) | 0.78 | | 0.866 | 0.075 | -0.060 | 0.006 |

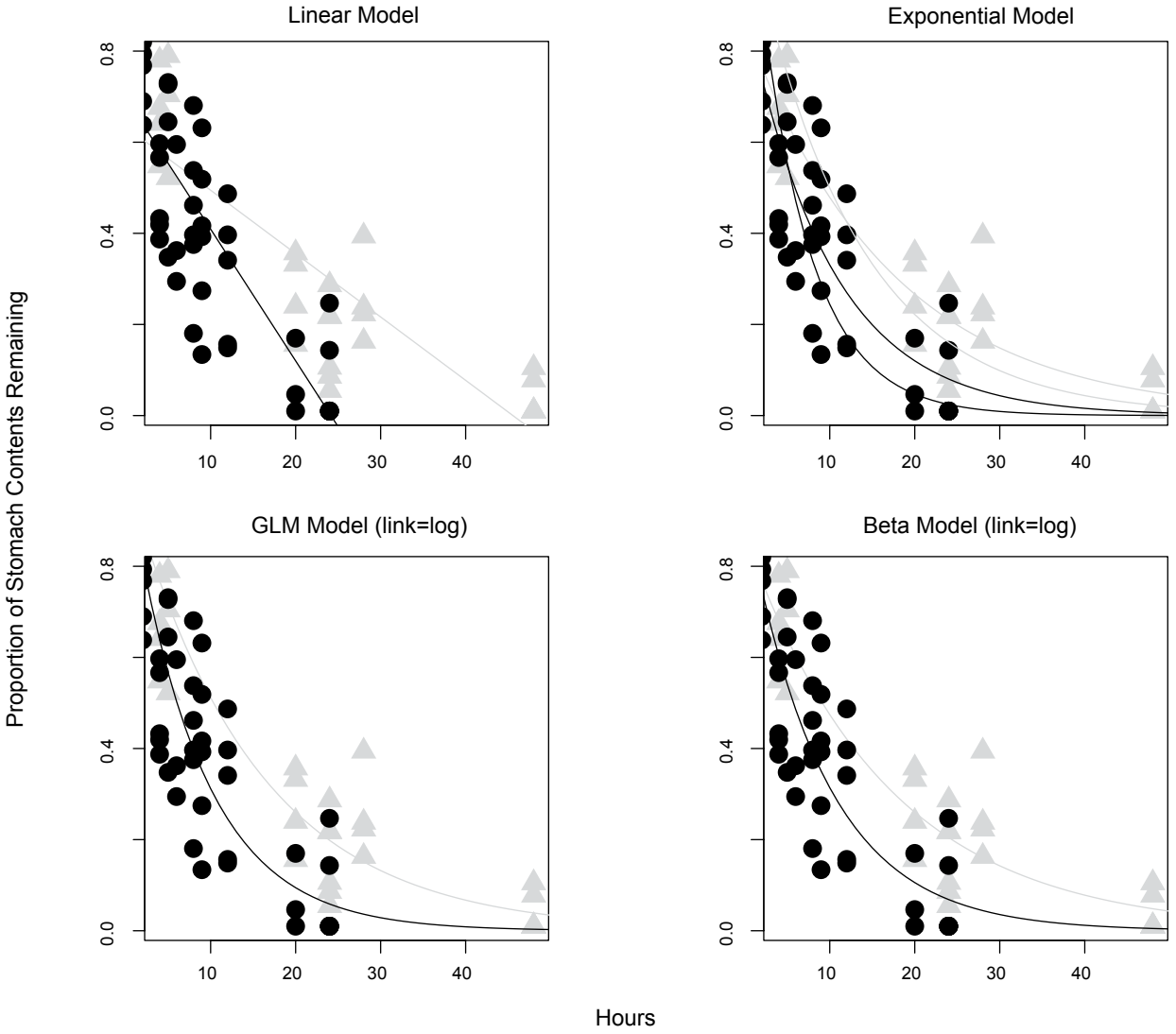


Fig. 2. Clearnose Skate, *Leucoraja eglanteria:* Estimated functions using different methods to fit proportion of stomach contents remaining over time, at 20ºC (black filled circles) and 15ºC (gray filled triangles).

gastric lavage was very effective on Winter Skates with piscine or crustacean prey.

Bromley (1988, 1994) concluded that exponential evacuation rate models could be misleading and that evacuation in most species of fish is actually linear. Our evaluation of the linear model did not support Bromley's (1988) assertion. However, there are a number of modern statistical approaches that allow non-normal data distributions to be modeled. The Gamma distribution assumes values are positive (0 to ∞) and the Beta distribution assumes values ranged between 0 and 1. A statistical evaluation of the different methods is beyond the scope of this paper, but all the approaches for fitting the exponential model yielded similar results and fit the data better than the linear model.

Evacuation rates derived here for Clearnose Skate are similar to those estimated for other *Leucoraja* skates when the exponential models are compared. Skates of the genus *Leucoraja* have similar body shapes, food search behaviors, and possibly comparable activity levels and metabolic rates. When fed small fish, all three species studied to date (Little Skate, Nelson and Ross, 1995; Winter Skate, Wunder, 1995; Clearnose Skate, this study), exhibited rapid commencement of digestion and some variability in rates of digestion among individuals. Although Nelson and Ross (1995) found the best fit for

Table 2. Comparison of evacuation rates of Clearnose (*Leucoraja eglanteria*), Little (*L. erinacea*), and Winter Skate (*L. ocellata*), number of runs (*n*), length range, temperature, and prey, reporting the exponential models of evacuation rate from each study for consistency.

| Species | *n* | Length (cm) | Temp. | Prey | Evacuation rate (R. exponential model) | Study |
|---|---|---|---|---|---|---|
| Clearnose Skate | 47 | 57–73 cm | 20 °C | whole Sand Lance | 0.102 | Stehlik *et al*. (this study) |
| Clearnose Skate | 28 | 57–73 cm | 15 °C | whole Sand Lance | 0.059 | Stehlik *et al*. (this study) |
| Little Skate | 17 | 33–51 cm | 10 °C | whole Sand Lance | 0.056 | Nelson and Ross (1995) |
| Winter Skate | 28 | 40–100 cm | 10 °C | 1 Sand Lance | 0.057 | Wunder (1995) |
| Winter Skate | 35 | 40–100 cm | 10 °C | 2 Sand Lance | 0.056 | Wunder (1995) |
| Winter Skate | 27 | 40–100 cm | 10 °C | 3 Sand Lance | 0.046 | Wunder (1995) |
| Winter Skate | 27 | 40–100 cm | 14 °C | 2 Sand Lance | 0.071 | Wunder (1995) |

evacuation of Sand Lance at 10° by Little Skate was the square root model, in our study, the exponential model best described the evacuation rates in Clearnose Skates at both temperatures. Studies with Winter Skate indicate that crustaceans may be evacuated more slowly than fish (Wunder, 1995) and this result is also found in other studies (see Durbin *et al*., 1983). Curvilinear functions better described the evacuation of shrimp by Winter Skate due to a delay in commencement of digestion (Wunder, 1995). Age of the fish, stage of sexual development, mode of ingestion, and structure of the prey also contribute to rapidity of digestion. In this experiment, we reduced variability in evacuation rates from confounding factors by using only one food type and only male skates above a minimum size.

Temperature had a significant effect on evacuation in Clearnose Skate; the evacuation rate was higher at 20°C than 15°C. Temperature has a major influence upon digestion rates due to its effects on biochemical reactions, and evacuation rates increase as temperature increases (Durbin *et al*., 1983). When temperature was increased, evacuation rate also increased in other skates (Nelson and Ross, 1995; Wunder, 1995). Comparing among the three skate species studied to date indicate a similar temperature dependence in evacuation, but a greater number of species will need to be studied to verify interspecific similarities and differences.

The impact of consumption by elasmobranchs upon prey species in the Northeast U.S. Shelf Ecosystem may be substantial. Estimates for total consumptive demand by Clearnose Skate ranged between 2 000 and 18 000 mt/year during the 2000s (Link and Sosebee, 2008). Clearnose Skate is among the top 50 species caught in NEFSC bottom trawl surveys from 1968–2006, though less in biomass than Winter (*Leucoraja ocellata*), Little (*L. erinacea*), and Thorny Skates (*Amblyraja radiata*) (Lucey and Nye, 2010). The seven northeast U.S. skate species currently are managed together as a complex, but because each species has a particular thermal range and life history (Hogan *et al*., 2013), they may be managed separately in the future. Clearnose Skates are unique in that they are a warmer-water species and more abundant in the Mid-Atlantic Bight (Woodland *et al*., 2011).

Skate consumptive removals are a means to add ecological considerations to stock assessments and multi-species food web models (Link and Sosebee, 2008). Results

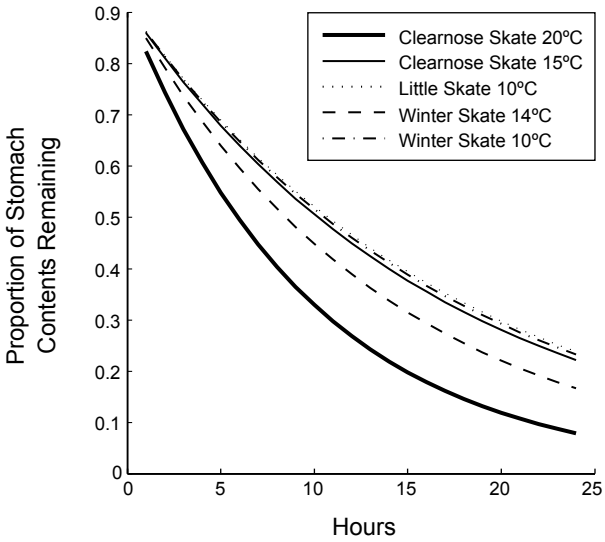


Fig. 3. Evacuation rates (R) of *Leucoraja* skates consuming small fish at various temperatures (Little Skate, Nelson and Ross, 1995; Winter Skate, Wunder, 1995).

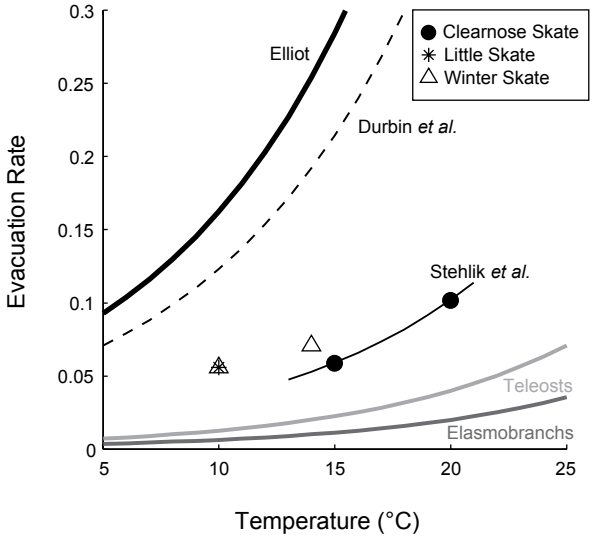


Fig. 4. Comparison of temperature-dependent evacuation rate for Clearnose Skate (this study, black line) and estimates from two other skate species: Little Skate (Nelson and Ross, 1995), Winter Skate (Wunder, 1995). Also shown are two earlier temperature-dependent functions: Atlantic Cod (dotted black line, Durbin *et al.*, 1983) and Brown Trout (Elliott, 1972) (thick black line). The slopes among Clearnose Skate ($b$ = 0.109), Brown Trout ($b$ = 0.112), and Atlantic Cod ($b$ = 0.111) are also very similar, the y-intercepts however are different: Clearnose Skate ($a$ = 0.011), Brown Trout ($a$ = 0.053) and Atlantic Cod ($a$ = 0.041). The sub-class evacuation rate functions used in many of the multispecies models in the region are also shown: teleost (light gray line) and elasmobranch (dark gray line).

of this study for Clearnose Skate and those of Little and Winter Skate can be used to develop a general evacuation rate function for skates or to reestimate overall consumption by skates in the ecosystem. Consumption is typically estimated as a function of mean stomach content weight and evacuation rate (Durbin *et al.*, 1983). In the Northeast U.S. Shelf Ecosystem, decades of field work have been conducted to quantify stomach contents in multiple species (Smith and Link, 2010), yet relatively few estimates of evacuation rate have been generated (Fig. 4). A greater emphasis should be given to estimating evacuation rates for additional species with an evaluation of Order or Family-level concurrence in evacuation rates. Further, a review of evacuation rates is also warranted. Newly measured evacuation rates and a synthesis of past work could be used to improve upon the sub-class-level estimates typically used in multispecies models in the region (Overholtz and Link, 2007; Link *et al.*, 2008).

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# Bottom Fish Assemblages at the Shelf and Continental Slope off East Greenland

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## Abstract

During 2006 and 2008 two bottom trawl surveys were conducted at East Greenland to 72°N covering depths down to 1500 m. In the 149 trawl hauls in total 113 fish species were recorded of which 37 were considered pelagic and excluded from the analyses. As a first step the abundance data for the 76 benthic species were used for analyses of the fish fauna diversity and fish assemblages. Nine assemblages were found by a standard type of cluster analysis. A Bayesian multinomial logit model was then applied to calculate vectors of probabilities defining the likelihood of each haul belonging to each of the nine clusters. By means of a geostatistical tool the spatial distribution of the conditional probabilities for each cluster (assemblage) was mapped. Each of the nine assemblages was further defined by indicator species, depth and temperature. The assemblages were well defined regarding geographical distribution, species composition, temperature and depth. Three of the assemblages were located in the cold Iceland Sea while six were found in the somewhat warmer Irminger Sea.

*Keywords*: Bayesian multinomial logit model, East Greenland, bottom fish assemblage, mapping

## Introduction

The water masses in the Iceland Sea and the Irminger Sea are to some extend separated by a submarine ridge between Iceland and Greenland (Dohrn Bank) with a maximum depth of 630 m (Fig.1). In the shelf area closest to East Greenland north of the ridge the hydrographical conditions are dominated by the southward flowing cold East Greenland Current which, to a large extend, is composed of Norwegian Deep Sea Water with temperatures often below 0°C (Buch, 2000). The hydrographical conditions in the southern part of the Denmark Strait and the Irminger Sea are influenced by two main currents bringing water masses of different origin into the area. The shelf is influenced by the cold East Greenland Current while the continental slope is dominated by inflow of warm (3.5–4.5°C), water from the Irminger Sea. The middle and lower part of the slope in the Irminger Sea is, however, also influenced by overflow over the submarine ridge of Northwest Atlantic Bottom Water (about 1°C) formed by cold Norwegian Deep-Sea Water.

Very little research on the total fish fauna and its distribution has been conducted in East Greenland waters. Haedrich and Kreft (1978) described the distribution of bottom fishes in the Denmark Strait and Irminger Sea based on 27 trawl hauls of which only about half were in East Greenland waters. Rätz (1999) identified a number of assemblages at depths between 0 and 400 m but his analyses were focused on commercial species. In recent years a number of checklist have been published covering also East Greenland waters (Møller *et al*., 2010, Mecklenburg *et al*., 2011, Christiansen *et al*., 2013), but none of these treat the detailed diversity and structure in the East Greenland fish fauna. The structure of the West Greenland fish fauna is better known due to detailed studies by *e.g.* Jørgensen *et al*. (2005, 2011),

In 2006 Greenland Institute of Natural Resources (GINR) conducted a bottom trawl survey between 67°N (north of Dohrn Bank) to 72°N including 10 trawl stations in Scoresby Sound and in 2008 GINR, for the first time, conducted a bottom trawl survey that covered both the

shelf and the continental slope between 59°45'N (Cape Farwell) and 67°N (Fig.1). Both surveys covered depths down to about 1500 m.

The purpose of the present study is to identify and describe fish assemblages at East Greenland and provide a baseline study in a region from which there is very little information and that is experiencing environmental changes owing to climate changes and that is under steadily anthropogenic impact mainly in the form of commercial fishery. The study will give a basis for a better understanding of spatial and temporal variability in the ecosystem in the future. This is done by identifying and mapping bottom fish assemblages by methods that are reproducible, hence future changes in assemblage composition and distribution can be statistically tested. The approach makes the results comparable to similar studies have been conducted in the Davis Strait (Jørgensen *et al*., 2005) and in the Baffin Bay (Jørgensen *et al*., 2011).

## Material and methods

Two depth stratified random bottom trawl surveys were conducted at East Greenland between 59°42'N and 71°54'N, with a total of 151 valid stations (Fig. 1). The survey area was stratified in 200 m depth intervals except a stratum from 1401–1500 m. Each stratum was allocated at least two hauls. The hauls were allocated by a method that combines the use of a minimum between-stations-distance rule (buffer zone) with a random allocation scheme (Kingsley *et al*. 2004). Both surveys were conducted by GINR's R/V *Paamiut* (722 gross tons).

During 16 – 26 September, 2006, 52 stations, including 10 stations in Scoresby Sound, were sampled north of Dohrn Bank (Northern area in Fig. 1), using an Alfredo III bottom trawl with a mesh size of 140 mm and a 30-mm mesh-liner in the cod-end. Further, 99 stations were sampled between Dohrn Bank and Cape Farwell (Southern area in Fig. 1) during 18 August–13 September, 2008, using a Cosmos 2000 shrimp trawl with a 20-mm meshliner in the cod end at depths < 600 m and an Alfredo III trawl at depths > 400 m. Both trawls were mounted with a rock hopper type ground gear. Towing speed was between 2.5 and 3 knots and towing time between 15 and 30 min. The exact wingspread, towing speed and towing time was recorded for each tow. The depth of the trawling ranged from 118–1460 m. Near-bottom temperatures were measured at all trawl stations, in 0.1°C increments, by a Seamon sensor (Starr-Oddi, 104 Reykjavik, Iceland) mounted on a trawl door. The catch at each station was sorted by species, counted and weighed to the nearest 0.1 kg. In total, 37 species considered as pelagic according to Whitehead *et al*. (1984–1986) were excluded from the analyses because an unknown fraction of the captured specimens might have been taken during setting and hauling of the trawl (Appendix A).

Abundance estimates were standardized to 1 km$^2$ swept area prior to further calculations using the exact wing spread, towing speed and towing time. The catchability is unknown and likely varies from species to species but in the present analysis it is set to 1.0, *i.e.*, all demersal fish within the trawled area were caught.

To identify fish assemblages within the survey area and to construct a map of their distribution, an approach somewhat similar the one proposed by Souissi *et al*., (2001) and further developed by Jørgensen *et al*. (2005) was applied. By means of a Bayesian multinomial logit model (Congdon, 2001) the probability that individual samples (trawl hauls), characterized by the particular composition of species and their abundances, belong to each of the groups of hauls (Assemblages) as defined by

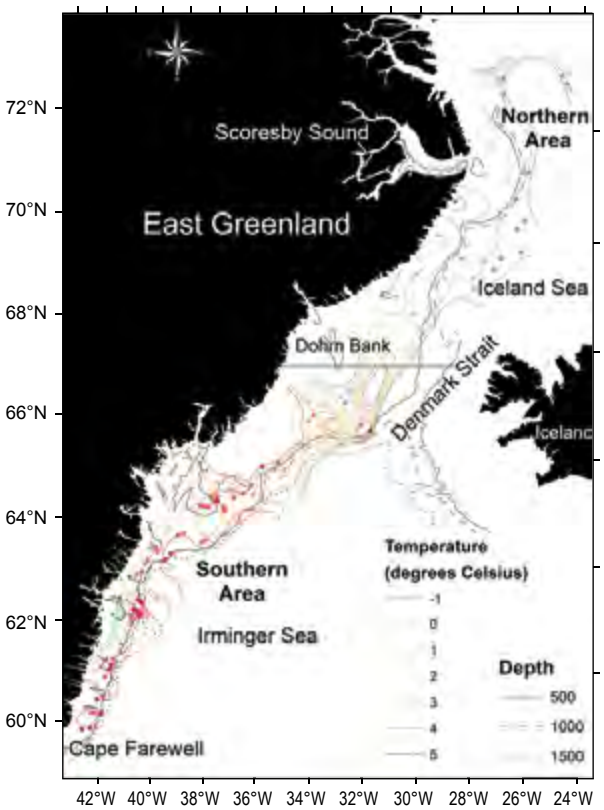


Fig 1. Survey area with distribution of trawl stations, indication of the northern and southern area (see text) and distribution of bottom temperatures based on interpolation by the spline method (regularized), with a weight of 0.1 and 12 points and a cell size on 5x5 km.

a multivariate cluster analysis was quantified. Each haul could thus be characterized by a geographical position and a vector of group membership probabilities. This provided the basis for drawing a continuous map of distribution using kriging (see below).

To reduce "noise", we selected only demersal species that were represented in more than 5% of the tows for analyses. The sum of the total abundance was estimated and species contributing more than 0.1% of the total sum were considered as primary species ($n$ = 25), whereas the remaining were classified as secondary species ($n$ = 12). The remaining 39 rare species (observed in less than 5% of the hauls (8)), of the 76 demersal species recorded, are not included in the analyses, but ranges of recorded depth, temperature and latitude are provided for all species in Appendix A.

Two stations were excluded from the assemblage analysis because they did not include any "Primary species". In total, 149 stations were hence used for further analysis.

***Cluster analysis***

The cluster analysis is a numerical rather than a statistical procedure and no assumption of normality is required. However, the data were transformed by a double square root in order to stabilize the variance and hence make the cluster analysis more robust. Further, the fourth root transform handles zeroes quite well as compared to log transforms which requires adding a subjectively chosen positive.

In the first step, the individual trawl hauls represented by data vectors (root four transformed counts of individuals of the 25 primary species $km^{-2}$) were analysed by multivariate cluster analysis using the Primer software v. 5.2 (Primer, 2001). The similarity coefficients between sites (trawl stations) were estimated by means of the Bray-Curtis clustering method (Legendre and Legendre, 1998).

The hierarchical tree obtained from the cluster analysis was split stepwise into an increasing number of "cut off levels", each time expanding the spatial organization patterns of the assemblages by one (*i.e.*, the first "cut off level" split the data set in two clusters, the second in three and so on). The procedure was stopped when there was no further increase in the "indicator values" (see Characterization of the assemblages (indicator values) below) indicating that no additional information was obtained by further subdividing the data set. (see Appendix 2 for the stepwise hierarchical split and Jørgensen *et al*., 2005)

***Bayesian multinomial logit model***

Once the numbers of clusters and their members have been determined, a probability that an individual haul is drawn from each of the clusters can be calculated. This was done using Bayesian multinomial logit model described by (Congdon 2001) and the mathematical formulation used for the present estimations is given in Jørgensen *et al*. (2005).

***Spatial distribution of assemblages***

A map of assemblage distribution could be constructed from the estimated probability vectors assigned to the geographical position of the haul. An interpolated regular grid, 0.025 longitude by 0.025 latitude degrees, was obtained by using a spherical variogram model and the kriging method (Matheron 1962, Souissi *et al*., 2001).

The kriging procedure provides estimates far from points with observations and thus also for areas that cannot be considered represented by the survey. Hence we have chosen to mask the maps of the conditional probabilities at approximately the 1700 m depth contours, a few hundred meters beyond the area covered by the surveys. All stations have a probability to belong to one of the nine clusters, although it often is very low. In order to improve the graphical representation areas with less than 15% conditional probability have been removed.

***Characterization of the assemblages (indicator values)***

Dufrêne and Legendre (1997) defined an index which was maximum (100%) when the individuals of a particular species are observed in all sites (trawl hauls) of only one assemblage; therefore the indicator value (IV) for any given species will be highest for the assemblage where it occurs in the greatest number of sites and this species could then be considered an "indicator species" for that assemblage. The indicator values were calculated for all primary and secondary species across all "cut-off levels" and assemblages after the reallocation of hauls (Jørgensen *et al*., 2005).

The indicator values were also used to assess the benefit of adding additional "cut-off-levels" to the initial cluster analysis. When no increase in indicator value was observed for any species no additional "cut-off-levels" were applied.

Mean temperature and depth with Standard Deviation and 95% confidence intervals is estimated by assemblage.

## Results

A total of 113 fish species were recorded during the surveys, of which 37 were considered pelagic and excluded from the analysis (Appendix 1).

The cluster analysis based on the 25 primary species defined nine groups of hauls with similar species

composition and density. The indicator values calculated for each species (before the reallocation of stations) within these nine clusters suggested that no additional information could be obtained by further separating the data *i.e.* the maximum indicator value observed for any given species did not increase by adding another "cut-off level".

The reallocation of hauls to the cluster to which they showed the highest probability of membership resulted in nine different assemblages with a rather well defined geographic distribution with statistically significant differences in mean depth or temperature or both.

The first "cut-off level" separates the nine groups in two, one with three groups or assemblages containing hauls all located in the Iceland Sea north of Dohrn Bank (Northern area in Fig 1), and one with six assemblages containing hauls all, except one, located in the Irminger Sea south of Dohrn Bank (Southern area Fig.1).

**Iceland Sea**

Assemblage 1 is located in deep (mean 1148 m) cold water (mean 0.0°C) on the slope (Fig 2; Table 1). *Gaidropsarus argentatus* (IV = 66.3) is the primary indicator species for this area where *Amblyraja hyperborea* also is an important species. The species *Lycodes paamiuti* (IV = 15.6), *Paraliparis bathybius* (IV = 33.6) and *Rhodichthys regina* (IV = 24.8) are secondary indicator species and are almost exclusively found in this area. Otherwise there are relatively few species here (Table 1).

Assemblage 2 is located in relatively shallow water (mean 485 m) with a mean temperature on 0.9°C along the coast and in Scoresby Sound. *Triglops nybelini* (IV = 90.2) and *Liparis fabricii* (IV = 74.2) are primary indicator species in this assemblage where *Artediellus atlanticus* is common, too (Fig. 2; Table 1). *Leptagonus decagonus* is secondary indicator species in this assemblage.

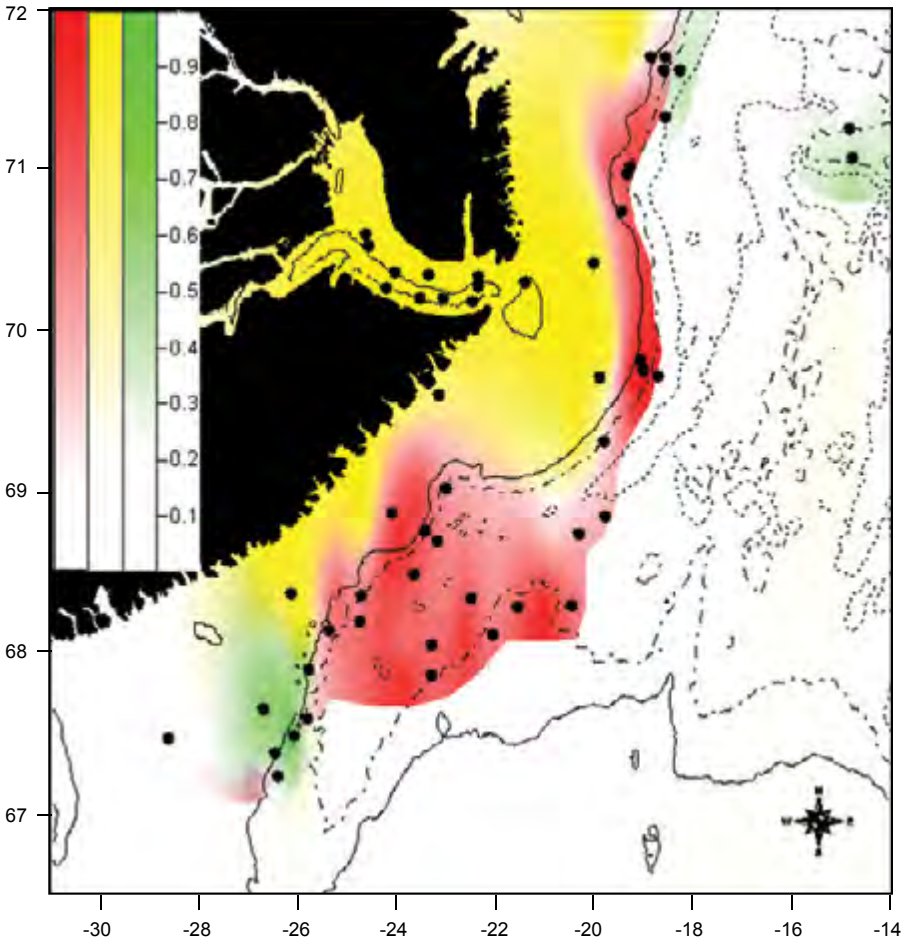


Fig 2. Northern area. Iso-probability map representing the spatial distribution of the possibility of belonging to Assemblages 1-3. 1:) 2:) 3:). Depth contours: 500 m solid, 1000 m dashed 1500 m dotted.

Table 1. Indicator values for primary and secondary indicator species and mean depth (m) and temperature °C with standard deviation and 95% confidence intervals by assemblage. n = number of hauls. Indicator species are given in bold.

| Assemblage | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| n | | 20 | 23 | 8 | 10 | 16 | 14 | 17 | 11 | 30 |
| Temperature | mean | 0.0 | 0.9 | 0.7 | 4.0 | 2.4 | 4.5 | 3.6 | 4.4 | 4.1 |
| | SD | 0.4 | 0.7 | 0.7 | 0.7 | 1.2 | 0.6 | 1.4 | 1.1 | 1.2 |
| | CI95 | 0.2 | 0.3 | 0.5 | 0.4 | 0.6 | 0.3 | 0.7 | 0.7 | 0.4 |
| Depth | mean | 1148.0 | 484.6 | 643.5 | 1110.4 | 835.3 | 404.3 | 599.9 | 190.4 | 311.6 |
| | SD | 238.4 | 185.3 | 286.8 | 219.1 | 118.6 | 40.1 | 139.5 | 36.2 | 90.9 |
| | CI95 | 104.5 | 75.7 | 198.7 | 135.8 | 58.1 | 21.0 | 66.3 | 21.4 | 32.5 |
| Primary speciees | | Indicator values | | | | | | | | |
| *Centroscyllium fabricii* | | 0 | 0 | 0 | 27.4 | 15.4 | 0 | 1 | 0 | 0 |
| *Amblyraja fyllae* | | 0 | 0 | 0 | 0.7 | 1.6 | 23.3 | 19.6 | 0 | 0 |
| *Amblyraja hyperborea* | | 56.3 | 7.3 | 21.5 | 0.2 | 0 | 0 | 0 | 0 | 0 |
| *Amblyraja radiata* | | 0 | 13.3 | 3.2 | 0.4 | 1.8 | 1.2 | **24.2** | 0 | 0.8 |
| *Synaphobranchus kaupi* | | 0 | 0 | 0 | **95.7** | 1.3 | 0 | 0 | 0 | 0 |
| *Notacanthus chemnitzii* | | 0 | 0 | 0 | 9.3 | 56 | 0 | 0 | 0 | 0 |
| *Trachyrhynchus murrayi* | | 0 | 0 | 0 | **70** | 0 | 0 | 0 | 0 | 0 |
| *Coryphaenoides rupestris* | | 0 | 0 | 0 | **97.2** | 0.9 | 0 | 0 | 0 | 0 |
| *Macrourus berglax* | | 0.1 | 0 | 1.7 | 39.6 | 48.9 | 0.3 | 2.2 | 0 | 3.2 |
| *Gadus morhua* | | 0 | 0 | 0 | 0 | 0 | 7.5 | 0 | **73.8** | 15.6 |
| *Melanogrammus aeglefinus* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5.8 | 44.6 |
| *Gaidropsarus argentatus* | | **66.3** | 0.1 | 24 | 0.4 | 8.2 | 0.5 | 0.5 | 0.1 | 0 |
| *Molva dipterygia* | | 0 | 0 | 0 | 9 | 2.3 | **50.3** | 1.9 | 0 | 0.8 |
| *Antimora rostrata* | | 0 | 0 | 0 | **99.6** | 0 | 0 | 0 | 0 | 0 |
| *Lepidion eques* | | 0 | 0 | 0 | **25.7** | 4.2 | 0 | 8.5 | 0 | 0 |
| *Anarhichas lupus* | | 0 | 0 | 0 | 0 | 0 | 2.9 | 0 | 18.7 | 24.7 |
| *Sebastes mentella* | | 0 | 0 | 0 | 0 | 1.5 | 90 | 7.6 | 0 | 3.1 |
| *Sebastes marinus* | | 0 | 0 | 0 | 0.1 | 0 | 20.5 | 0 | 2.8 | **64.8** |
| *Artediellus atlanticus* | | 0 | 52.4 | 5.2 | 0 | 0 | 0 | 0 | 0.6 | 0.1 |
| *Triglops murrayi* | | 0 | 0 | 0 | 0 | 0 | 1.3 | 0.2 | 13.8 | 8.4 |
| *Triglops nybelini* | | 0 | **90.2** | 0 | 0 | 0 | 0 | 0 | 0.2 | 0 |
| *Cottunculus microps* | | 2.6 | 5.8 | **63.3** | 0 | 0.1 | 0.3 | 0.6 | 0 | 0.1 |
| *Liparis fabricii* | | 3.3 | **74.2** | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hippoglossoides platessoides* | | 0 | 1 | 0 | 0 | 0 | 11.4 | 1.2 | 12.5 | 33.6 |
| *Reinhardtius hippoglossoides* | | 0 | 9 | 15.7 | 73.2 | 5.2 | 0.1 | 7.3 | 0 | 0.6 |
| Secondary species | | | | | | | | | | |
| *Bathyraja spinicauda* | | 0 | 0 | 0 | 3.5 | 29.1 | 2.8 | 1 | 0 | 0 |
| *Brosme brosme* | | 0 | 0 | 0 | 0 | 5.2 | 14.3 | 3.2 | 0 | 4.9 |
| *Anarhichas denticulatus* | | 0 | 0 | 0 | 5.2 | 5.3 | 8.5 | 5.9 | 0.8 | 5.7 |

Table 1 cont'd

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Anarhichas minor* | 0 | 0 | 8.1 | 1.1 | 0 | 6.1 | 0.1 | 5.4 | 10.2 |
| *Lycodes eudipleurostictus* | 10.7 | 10.4 | 0.7 | 0 | 0.6 | 0 | 3.2 | 0 | 0.7 |
| *Lycodes paamiuti* | **15.6** | 0 | 2.8 | 0 | 0.7 | 0 | 0 | 0 | 0.3 |
| *Lycodes pallidus* | 6 | 10.4 | 1 | 0 | 0 | 0 | 2.6 | 0 | 0.7 |
| *Lycodes reticulatus* | 0 | 16.8 | 13.9 | 0 | 0 | 0 | 0 | 0 | 0.1 |
| *Lycodes seminudus* | 5.4 | 2.9 | 5.9 | 0 | 0 | 0 | 1.9 | 0 | 0.3 |
| *Leptagonus decagonus* | 0 | **40.1** | 0 | 0 | 0 | 0 | 0.4 | 0 | 0.2 |
| *Careproctus reinhardti* | 24.8 | 4.8 | 15.6 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paraliparis bathybius* | **33.6** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Rhodichthys regina* | **24.8** | 0 | 15.3 | 0 | 0 | 0 | 0 | 0 | 0 |

Assemblage 3 is a group of eight hauls somewhat scattered in the area at intermediate depth (mean 644 m) and with a mean temperature at 0.7°C. *Cottunculus microps* is primary indicator species (IV = 63.3) for this assemblage and the commercially important species *Reinhardtius hippoglossoides* has also its highest densities in the northern area in this assemblage although the indicator value is low (IV = 15.7). Otherwise the assemblage is characterised by few primary species with low indicator values (Fig. 2, Table 1). Assemblage 3 is separated from the deeper Assemblage 1 by the high presence of *Cottunculus microps* and *Reinhardtius hippoglossoides* and relative low presence of *Gaidropsarus argentatus* and *Amblyraja hyperborea* and from the shallow Assemblage 2 by the presence *Cottunculus microps* and the absence of *Triglops nybelini* and *Liparis fabricii.*

**Irminger Sea**

Six of the nine assemblages are located in the Irminger Sea. Some of the assemblage have mean depths close to the assemblages defined in the Iceland Sea but the mean temperature is statistically significant (95% level) higher in all assemblages (Table 1).

Assemblage 4 is the deepest located assemblage in the southern area and is a rather well defined group of ten hauls at deep (mean 1110 m) and relatively warm water (4.0°C). The primary indicator species are the common deep water species *Antimora rostrata* (IV = 99.6), *Coryphaenoides rupestris* (IV = 97.2), *Synaphobranchus kaupi* (IV = 95.7), *Trachyrynchus murrayi* (IV = 70.0) and *Lepidion eques* (IV = 25.7). *Reinhardtius hippoglossoides* also has its highest indicator value for a single assemblage in this assemblage (Fig 3, Table 1) but the highest indicator value is found in Assemblage 4 and 5 combined (Appendix 2).

Assemblage 5 is the second deepest assemblage but found at statistically significant (95% level) shallower depth (mean 835 m) and temperature (2.4°C) than Assemblage 4 (Fig 4., Table 1). The assemblage has no indicator species but *Notacanthus chemnitzii, Macrourus berglax* and *Bathyraja spinicauda* have their highest indicator value for a single assemblage here but all three species are indicator species for Assemblage 4 and 5 combined (Appendix 2). Assemblage 5 is separated from Assemblage 4 by the absence of *Antimora rostrata* and *Trachyrynchus murrayi* and very few *Coryphaenoides rupestris, Synaphobranchus kaupi, Lepidion eques* and *Reinhardtius hippoglossoides*.

Assemblage 6 is found at mean depth of 404 m and mean temperature of 4.5°C. *Molva dipterygia* (IV = 50.3) is the primary indicator species and *Sebastes mentella* has by far its highest indicator value for a single assemblage here (IV = 90.0) although it is indicator species for Assemblage 6 and 7 combined (Appendix 2). The secondary indicator species *Brosme brosme* has also it highest indicator value for a single assemblage here (Fig 4., Table 1).

Assemblage 7 is the third deepest assemblage with a mean depth of 600 m and a mean temperature of 3.6°C. The depth is significantly different (95% level) from the deeper Assemblage 5 and the shallower Assemblage 6, while the temperature difference between the shallower and deeper assemblages is barely statistically different (95% level) (Table 1). The only primary indicator species is *Amblyraja radiata* (IV = 24.2) (Fig.5, Table 1). The Assemblage is separated from the deeper Assemblage 5 primarily by the presence of *Amblyraja radiata* and the absence of *Notacanthus chemnitzii* and *Macrourus berglax* and from the shallower Assemblage 6 by low indicator values of *Molva dipterygia* and S*ebastes mentella*.

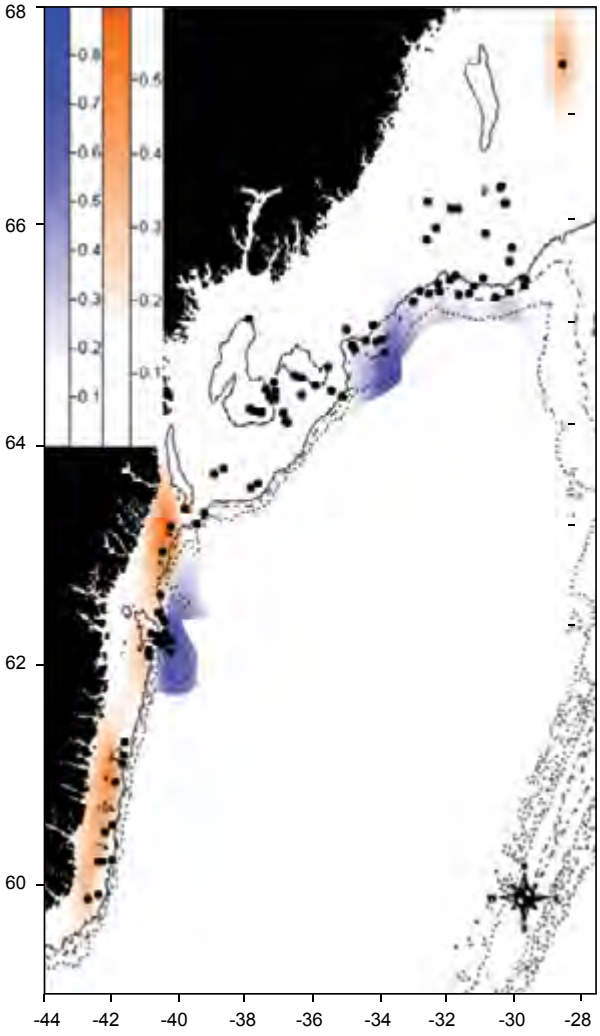


Fig 3. Southern area. Iso-probability map representing the spatial distribution of the possibility of belonging to Assemblages 4 and 8. Assemblage 4: ) and 8: ). Note difference in the scale. Depth contours: 500 m solid, 1000 m dashed, 1500 m dotted.

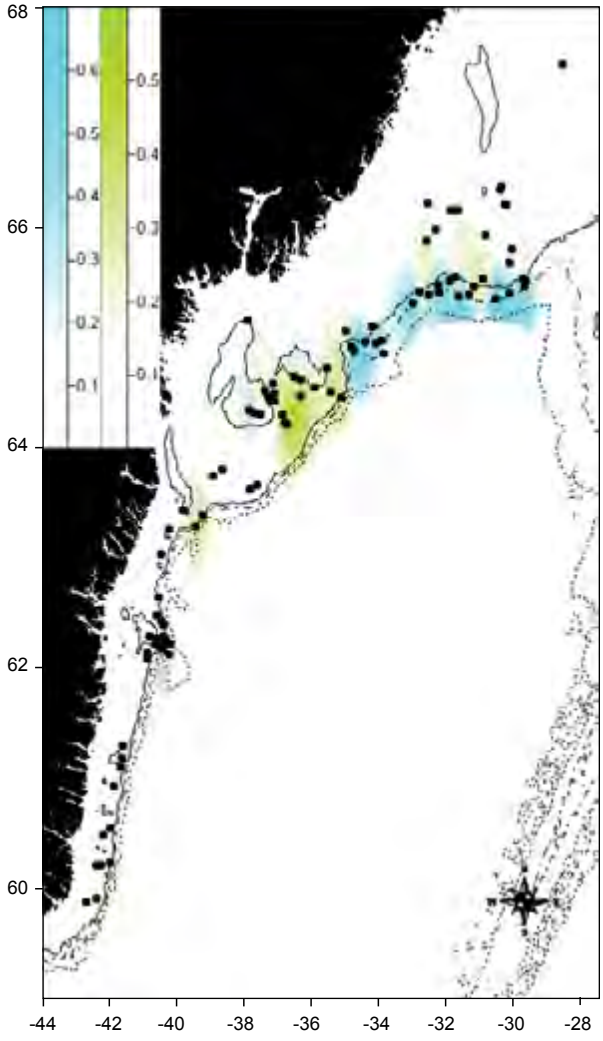


Fig 4. Southern area. Iso-probability map representing the spatial distribution of the possibility of belonging to Assemblages 5 and 6. Assemblage: 5 ) and 6: ). Note difference in the scale. Depth contours: 500 m solid, 1000 m dashed, 1500 m dotted.

Assemblage 8 is the shallowest located assemblage with a mean depth of 190 m and mean temperature of 4.4°C (Table 1). The assemblage is primarily located in the southern part of the survey area but single haul north of Dohrn Bank is also associated Assemblage 8 (Fig. 3). *Gadus morhua* is the only indicator species (IV = 73.8) and the assemblage is characterized by relatively few species with low indictor levels. The depth is significantly different from the slightly deeper Assemblage 9 from which it is separated mainly because of strong presence of *Gadus morhua* and few *Melanogrammus aeglefinus* and *Sebastes marinus* (Table 1).

Assemblage 9 is found all along the coast (Fig. 5) and has a mean depth of 312 m and a mean temperature of 4.1°C (Table 2). *Sebastes marinus* is the only primary indicator species (IV = 64.8) but *Anarhichas lupus*, *Melanogrammus aeglefinus* and *Hippoglossoides platessoides* have their highest indicator values for a single assemblage in this assemblage. The assemblages mean depth is significantly different (95%) from the shallower Assemblage 8 and the deeper Assemblage 6, while there is no statistical difference in mean temperature between the assemblages. Assemblage 9 is separated from Assemblage 6 by the high presence of *Sebastes marinus*, *Melanogrammus aeglefinus*

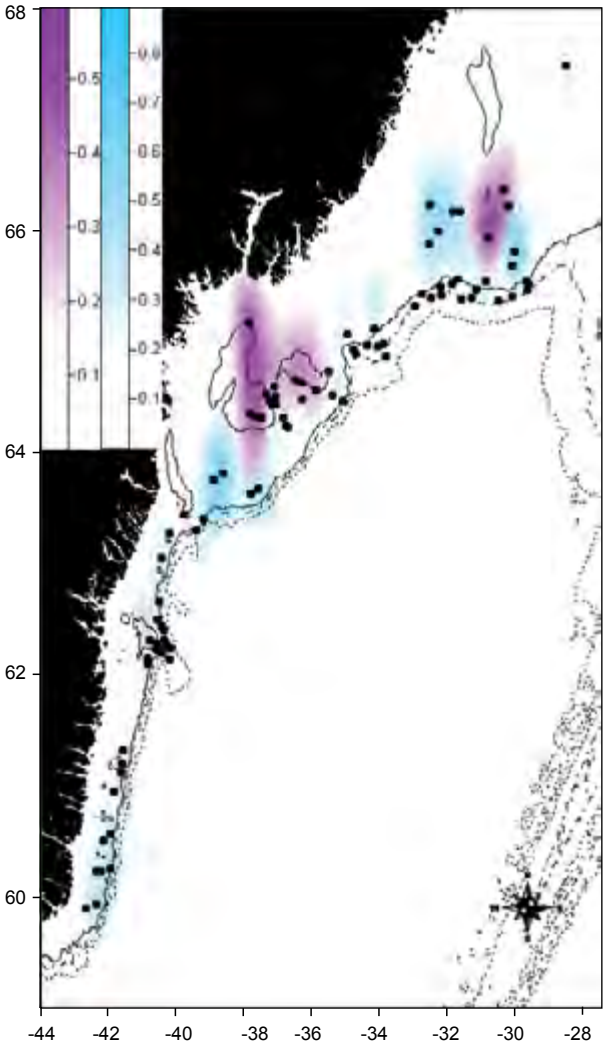


Fig 5. Southern Area. Iso-probability map representing the spatial distribution of the possibility of belonging to Assemblages 7 and 9. Assemblage 7: ) and 9: ). Note difference in the scale. Depth contours: 500 m solid, 1000 m dashed, 1500 m dotted.

and *Anarhichas lupus* in Assemblage 9 and high presence of *Molva dipterygia* and *Sebastes mentella* in Assemblage 6 while these species are rare in Assemblage 9.

A number of indicator species cannot be grouped within a particular assemblage but are more or less widespread throughout a number of assemblages. *Amblyraja hyperborea* (IV = 62.4) is primary indicator species for the three Assemblages (1–3) in the Iceland Sea, while *Careproctus reinhardti* (IV = 33.3), *Lycodes seminudus* (IV = 12.2), *L. eudipleurostictus* (IV = 21.2) and *L. pallidus* (IV = 15.5) are secondary indicator species for the same area (Appendix 2). *Macrourus berglax* (IV = 91.3), *Reinhardtius hippoglossoides* (IV = 76.6) and *Centroscyllium fabricii* (IV = 40.5) are primary indicator species and *Bathyraja spinicauda* (IV = 30.3) is secondary indicator species for the deepest part of the survey area in the Irminger Sea (Assemblage 4 and 5), while *Hippoglossoides plattessoides* (IV = 45.4) is generalist (eurytrophic) found widespread in the shallower Assemblages (6–9). Some species as *Sebastes mentella* (IV = 96.4) and *Amblyraja fyllae* (IV = 44.1) are assigned to intermediated depths (Assemblage 6 and 7) while others as *Anarhichas lupus* (IV = 46.2), *Melanogrammus aeglefinus* (IV = 51.1) and *Triglops murrayi* (IV = 17.6) are primarily found at shallow depths (Assemblage 8 and 9) (Table 2, Appendix 2).

The relative probability of finding one of the 25 primary species within one of the nine assemblages is provided in Table 2 (Jørgensen *et al.*, 2005). *Reinhardtius hippoglossoides* is found in eight out of nine assemblages and there is a relatively high probability of finding it in five out of the nine assemblages. The species has it highest probabilities in Assemblage 2 and 3 in the Iceland Sea, but the indicator value is relatively low (Table 1). This is caused by hauls with few species in low numbers. It should be noticed that abundance differences among assemblages are not included in these probabilities and the probabilities (or relative abundance) can only be used for direct comparison within assemblages. A species like *Sebastes mentella* is also found in a number of assemblages, but with the highest probability (0.60, 0.43) in Assemblage 6 and 7, respectively (medium deep water in the Irminger Sea, Table 2). Other species are only found within a few assemblage *e.g.*, *Antimora rostrata* and *Centrocyllium fabricii,* which are only found in the two deepest Assemblages in the Irminger Sea (Assemblage 4 and 5) and *Trachyrhynchus murrayi* which is exclusively found in Assemblage 4 (Table 2).

## Discussion

### Methods

The analyses are based on data from 2006 (northern area) and 2008 (southern area) (Fig. 1). Most of the species included in the analyses are long lived (Whitehead *et al*., 1984), and fishing pressure has been low north of Dohrn Bank from 2006 to 2008 (Anon., 2009). Further it is assumed that the bottom temperature in the northern area has been stable between 2006 and 2008 as in the southern area (Pers. Com. Kaj Sünksen, Greenland Institute of Natural Resources. Unpublished survey results). It is hence considered that the changes in species composition and abundance in the northern area between 2006 and 2008 has been insignificant.

Table 2. Estimated relative abundance of primary indicator species within the nine assemblages.

| Species | Assemblage | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| *Centroscyllium fabricii* | 0.000 | 0.000 | 0.000 | 0.046 | 0.032 | 0.000 | 0.005 | 0.000 | 0.000 |
| *Amblyraja fyllae* | 0.000 | 0.000 | 0.000 | 0.004 | 0.014 | 0.035 | 0.064 | 0.000 | 0.000 |
| *Amblyraja hyperborea* | 0.365 | 0.066 | 0.120 | 0.004 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| *Amblyraja radiata* | 0.000 | 0.038 | 0.049 | 0.004 | 0.021 | 0.009 | 0.099 | 0.000 | 0.006 |
| *Synaphobranchus kaupi* | 0.000 | 0.000 | 0.001 | 0.128 | 0.034 | 0.000 | 0.003 | 0.000 | 0.000 |
| *Notacanthus chemnitzii* | 0.000 | 0.000 | 0.001 | 0.031 | 0.095 | 0.000 | 0.000 | 0.000 | 0.000 |
| *Trachyrhynchus murrayi* | 0.000 | 0.000 | 0.000 | 0.076 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| *Coryphaenoides rupestris* | 0.000 | 0.000 | 0.001 | 0.176 | 0.039 | 0.003 | 0.000 | 0.000 | 0.000 |
| *Macrourus berglax* | 0.006 | 0.004 | 0.118 | 0.144 | 0.290 | 0.023 | 0.086 | 0.000 | 0.022 |
| *Gadus morhua* | 0.000 | 0.000 | 0.019 | 0.000 | 0.000 | 0.083 | 0.005 | 0.543 | 0.157 |
| *Melanogrammus aeglefinus* | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 | 0.005 | 0.109 | 0.067 |
| *Gaidropsarus argentatus* | 0.525 | 0.007 | 0.125 | 0.010 | 0.067 | 0.007 | 0.010 | 0.004 | 0.002 |
| *Molva diterygia* | 0.000 | 0.000 | 0.000 | 0.016 | 0.019 | 0.099 | 0.029 | 0.000 | 0.009 |
| *Antimora rostrata* | 0.000 | 0.000 | 0.000 | 0.112 | 0.005 | 0.000 | 0.000 | 0.000 | 0.000 |
| *Lepidion eques* | 0.000 | 0.000 | 0.000 | 0.040 | 0.014 | 0.000 | 0.010 | 0.000 | 0.000 |
| *Anarhichas lupus* | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.017 | 0.000 | 0.059 | 0.073 |
| *Sebastes mentella* | 0.000 | 0.000 | 0.000 | 0.010 | 0.177 | 0.599 | 0.436 | 0.000 | 0.242 |
| *Sebastes marinus* | 0.000 | 0.000 | 0.001 | 0.013 | 0.018 | 0.067 | 0.004 | 0.098 | 0.262 |
| *Artediellus atlanticus* | 0.000 | 0.123 | 0.052 | 0.000 | 0.000 | 0.000 | 0.000 | 0.004 | 0.002 |
| *Triglops murrayi* | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 | 0.004 | 0.002 | 0.057 | 0.009 |
| *Triglops nybelini* | 0.000 | 0.249 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.004 | 0.001 |
| *Cottunculus microps* | 0.031 | 0.060 | 0.232 | 0.000 | 0.004 | 0.005 | 0.010 | 0.000 | 0.001 |
| *Liparis fabricii* | 0.044 | 0.212 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| *Hippoglossoides platessoides* | 0.000 | 0.016 | 0.000 | 0.000 | 0.000 | 0.034 | 0.023 | 0.121 | 0.121 |
| *Reinhardtius hippoglossoides* | 0.028 | 0.223 | 0.276 | 0.185 | 0.168 | 0.013 | 0.209 | 0.000 | 0.027 |

**Note.** Values give the estimated probabilities of a a randomly drawn specimen from the assemblage belonging to each of the 25 species *i.e.*, the probability vectors characterizing the assemblage.

In 2008 there were used two different survey trawls with 20 and 30 mm mesh in the codend, respectively. There was a certain overlap in the depths were the two trawls where used (400–600 m) but there were too few hauls and they were located too far from each other to allow a firm conclusion about the difference in selectivity in the two gears. Bech (1994) compared the selectivity in codends on 20 and 44 mm, respectively, in West Greenland waters. There was no difference in selectivity for *Reinhardtius hippoglossoides* but there was a significant difference in selectivity for small redfish. The catchability for 10 cm redfish in a 20 mm cod end was 2.9 times higher than in a 44 mm cod end (no data for 11 cm redfish indicating that there was no difference in catchability in the two mesh sizes at that size). For comparison it is assumed that (red)fish > 9 cm are fully recruited to the 30 mm trawl. Fish less than 10 cm contributed 0.2 % of the catches in numbers at depths between 400 and 600 m in the 30 mm codend compared to 5.7% of the catches with the 20 mm codend. (62% of the catches were small redfish from a single haul). The trawl with the 20 mm codend covered depths shallower than 600 m where only 4.2 % of the caches were < 10 cm and 92.6 % of these small fish were *Sebastes mentella*. The abundance of *S. mentella* seems hence to be slightly overestimated in the 20 mm trawl compared to the 30 mm trawl but the difference in mesh size only have a very minor effect on the abundance estimates on other species. The overall distribution of *S. mentella* is probably not affected by the difference in mesh size while the relative distribution of indicator value

between Assemblage 6 (mainly covered by the 20 mm trawl) and Assemblage 7 (mainly covered by the 30 mm trawl) could be twisted slightly.

The bottom topography with either very rough and steep or very soft and muddy bottom that not allow bottom trawling, together with areas at the coast that not has been surveyed due to incomplete maps implies that there are areas with no information. This applies to the entire costal area and a rather large area with relatively shallow water between 64°N and 68°N and areas > 1000 m between 62°45'N and 64°N together with depths > 600 m south of 61°45'N. This results in incomplete distribution maps. This applies especially to Assemblage 4 (Fig. 3) but also Assemblage 5 (Fig 4). These two assemblages are composed of species found wide spread in the North Atlantic such as *Antimora rostrat*, *Coryphaenoides rupestris*, *Synaphobranchus kaupi*, *Trachyrhynchus murrayi, Centrocyllium fabricii, Notacanthus chemnizii* and *Macrourus berglax* (Whitehead *et al*., 1984–1986) and there is no reason to believe that these species should not be distributed all along the slope of the Irminger Sea.

For a discussion of the Bayesian multinomial logit model see Jørgensen *et al.* (2005)

## Results

The study shows that three of the identified assemblages are located north of Dohn Bank in the cold water in the Iceland Sea while six are located in the relatively warm Irminger Sea. The bottom fish fauna in Iceland Sea is hence to a large extend separated from the fish fauna in the Irminger Sea by the submarine sill between Iceland and East Greenland (Dohrn Bank) and there is little overlap in the species composition in the two areas. A similar separation between areas has also been shown for some fish families *e.g.*, Macroridae (Jørgensen 1996) and Zoarcidae (Møller and Jørgensen, 2000), and for the total fish fauna at West Greenland (Jørgensen *et al*., 2005).

One station from Assemblage 8, which is mainly found in the Irminger Sea, is, however, located in the Iceland Sea. This haul is associated to Assemblage 8 due to the presence of *Gadus morhua* and *Hippoglossoides platessoides* and general absence of species found in the three Iceland Sea assemblages. The station was the shallowest in the northern area (288 m) with a bottom temperature among the highest (1.4°C).

Haedrich and Krefft (1978) identified five assemblages in the Irminger Sea, Denmark Strait and Icelandic Sea based on 27 trawl hauls of which eight were located at the Icelandic slope, where the bottom temperatures generally were higher than at East Greenland. They also included pelagic species and generally the range in temperature and depth in the assemblages was much wider in their study which further complicates a direct comparison with the present study. Haedrich and Krefft (1978) identified an assemblage in the Iceland Sea (three hauls at 330–693 m, -0.7– 0.5 °C) dominated by *Reinhardtius hippoglossoides* which also is relatively important in Assemblage 3 in the present study. Their second most important species *Gadus morhua* was only observed in a single haul in the Icelandic Sea in 2006 but it is likely that this assemblage would have been more widespread north of the sill if the coverage of the shallow areas had been better.

A few other species as the highly migratory *Reinhardtius hippoglossoides* and species such as *Amblyraja radiata* and *Gaidropsarus argentatus* found widespread north and south of the sill indicating that they tolerate a wide range of temperatures including temperatures close to 0°C.

### Iceland Sea

In the Iceland Sea the three assemblages (1, 2 and 3) were different regarding mean temperature, mean depth and species composition. Assemblage 2 and 3 were however not significantly different (95% level) neither regarding temperature nor depths indicating that factors other than these two parameters *e.g.* bottom conditions, salinity, current strength etc. determines the distribution of the fish. The lack of statistical difference could also be caused by the relatively few observations in Assemblage 3.

It is generally difficult to compare fish assemblages from different areas, since they have usually been defined by different sampling gear and calculation methods. Jørgensen *et al*. (2005, 2011) identified, however, a number fish assemblage in the Baffin Bay and Davis Strait using same approach as presented here.

The shallowest assemblage (Assemblage 2) with the indicator species *Liparis fabricii*, *Triglops nybelini* and *Leptagonus decagonus,* and with a large presence *of Artediellus atlanticus,* resembles an assemblage in the Northern Baffin Bay with a mean depth at 459 m and mean temperature on 0.4°C where the three species also were indicator species, while *Liparis fabricii* was found widespread in cold the northern Baffin Bay (Jørgensen *et al*., 2011).

The assemblage at intermediate depth (Assemblage 3) has *Cottunculus microps* as indicator species. The species was also common at a similar depth (652 m) in the northern

Baffin Bay together with *Careproctus reinhardti* and *Lycodes seminudus* which also are common in the Iceland Sea (Jørgensen *et al*., 2011).

The deepest assemblage in the Iceland Sea (Ass.1) has *Gaidropsarus argentatus* as primary indicator species and *Lycodes squamiventer, Paraliparis bathybius* and *Rhodichthys regina* as secondary indicator species. *Gaidropsarus argentatus* is also found in the southern area but not in the Baffin Bay, where it is replaced by *G. ensis*. *Paraliparis bathybius* and *Rhodichthys regina* were indicator species for assemblages at similar depths (app. 1100 m) in both the northern and southern part of the Baffin Bay. *Amblyraja hyperborea* that is found widespread in the Iceland Sea is also found widespread in the Northern Baffin Bay (Jørgensen *et al.*, 2011) and is primary indicator species in the deepest assemblage in the southern Baffin Bay (Jørgensen *et al.*, 2005). *Amblyraja hyperborea* was also one of the dominating species in the "upper slope (cold) assemblage" defined by Bergstad *et al.* (1999). All in all the species composition especially in the northern Baffin Bay but also to a wide extend in the southern Baffin Bay resembles the species composition in the Greenland part of the Iceland Sea. In the shallower part of southern Baffin Bay there is, however, some southern distributed species brought to the area by the warm West Greenland Current (Jørgensen *et al.*, 2005). Assemblage 1 in the Iceland Sea have also considerable resemblance to the cold Arctic "Norwegian Sea Deep-water assemblage", depths ranging from 1498–2051 m, defined by Bergstad *et al.* (1999) from the slope of the eastern Norwegian Sea. The latter was dominated by *Lycodes frigidus*, of which only a few specimens were taken at negative temperature in the Iceland Sea and the two Liparids, *Paraliparis bathybius* and *Rhodichthys regina*, which are secondary indicator species in Assemblage 1.

**Irminger Sea**

In the Irminger Sea six different assemblages were identified, all at significantly (95% level) different depth. The temperature was, however, relatively uniform throughout the area and only Assemblage 5 was significantly colder than the two closest assemblages, Assemblage 4 and 7.

The medium depth Assemblages 6 and 7 (mean depths 404 and 600 m, respectively) resembles a similar assemblage (3.5°C and mean depth 525 m) in the Davis Strait and southern Baffin Bay where *Sebastes mentella* and *Hippoglossoides platessoides* are primary indicator species. *Sebastes mentella* is primary indicator species in Assemblage 6–7 while *Hippoglossoides platessoides* is found widespread in the four shallow assemblages in the Irminger Sea. The study in the Davis Strait did not cover depths < 400 m.

The deepest assemblage in the Irminger sea resembles a similar assemblage (3.6°C and mean depth 1104 m) in the Davis Strait where *Antimora rostrata, Coryphaenoides rupestris, Synaphobranchus kaupi* and *Centrocyllium fabricii*, that are found widespread in the North Atlantic, also were indicator species (Jørgensen *et al.*, 2005).

Rätz (1999) analysed the structures and changes of demersal fish assemblage off West and East Greenland at depths between 0 and 400 m during 1982–1996. The most abundant species were *Sebastes marinus, Sebastes mentella, Gadus morhua, Hippoglossoides platesoides, Anarhichas lupus* and *Amblyraja radiata*, which also are common in the shallow Assemblages 6, 8 and 9 in the present study. Rätz focused on abundance, biomass and mean weights and it is hard to make any further comparisons with the present study regarding changes in the composition of demersal fish assemblages in the intervening years.

Haedrich and Krefft (1978) identified an assemblage (493–975 m, 0.1–3°C) resembling Assemblage 5 in temperature and depth where *Macrourous berglax, Coryphaenoides rupestris, Antimora rostrata* and *Gaidropsarus argentatus* where the most dominant species. Assemblage 5 is to a large extend defined by the absence of a large number of species and the species Haedrich and Krefft mention are dominant species in the deep Assemblage 4 while *Gaidropsarus argentatus* is dominant species in the cold deep Assemblage 1 and rare in the Irminger Sea. Haedrich and Krefft also defined an assemblage (763–1502 m, 3.9–5.6°C) resembling Assemblage 4 which included *Coryphaenoides rupestris* and *Lepidion eques* that also are dominant species in Assemblage 4. Further their assemblage included *Sebastes mentella* which not is present in Assemblage 4. Whether the general deeper distribution of some species (*Macrourous berglax* and *Antimora rostrata*) more northern (*Gaidropsarus argentatus*), more southern (*Gadus morhua*) or shallower (*Sebastes mentella*) distribution in the present investigations compared to the distributions described by Haedrich and Krefft (1978) are caused by changes in the environment or due to the relatively few observations in their study is not clear.

In their investigation of the fish assemblages off eastern Canada and USA Mahon *et al*. (1998) defined a "Northern Deep Water assemblage" which had the species *Antimora rostrata, Coryphaenoides rupestris, Synaphobranchus kaupi, Notacanthus chemnitzi* and *Macrourus berglax*

in common with the two deepest assemblages in the Irminger Sea (Assemblage 4–5). These species are widely distributed in the North Atlantic (Whitehead *et al*., 1984–1986), but it is worth noting that the mean depth was 537 m (however with a large variance) with a mean temperature of 4.1°C in Mahon *et al*. (1998) compared to a mean depth of 1110 m and 3.9°C in the present investigation. This suggests a shift to deeper waters in far northern areas for these species that may be related to temperature preferences.

The present study confirms that depth and oceanographic features (mainly temperature) is the most important factors in separating fish assemblages in the North Atlantic and World-wide (Gomes *et al*., 1995). The equal importance of depth and temperature at East Greenland is in accordance with Haedrich and Krefft (1978) who suggested that the slope fish fauna of the temperature-unstable Denmark Strait is structured by both depth and temperature. At the even more temperature extreme Norwegian shelf, major importance of temperature as the separating factor of fish assemblages was hypothesized by Bergstad *et al*., (1999) and Bjelland *et al*., *(*2000). The major importance of depth and minor contribution of temperature in defining the distribution patterns at both East and West Greenland is in accordance with studies from other areas with limited temperature gradients *e.g.* New England (Haedrich *et al*., 1975) and Rockall Trough (Gordon and Duncan 1985). At East Greenland temperature only had a significant influence on the distribution of the fish between the cold Iceland Sea and the warm Irminger Sea. Within the areas depth seem to be the most dominating parameter regarding the distribution of the fish fauna.

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## Appendix 1.

Species list from two surveys at East Greenland in 2006 and 2008, respectively. Status:"p" considered pelagic. Number: Maximum number caught in a single haul. Depth: Minimum and Maximum depth (m). Temperature; Minimum and maximum temperature °C. and maximum northern latitude.

| | | | Depth | | Temperature | | Northern |
|---|---|---|---|---|---|---|---|
| Species | Status | Number | Min | Max | Min | Max | Latitude |
| *Petromyzon marinus* (Sea lamprey) | | 3 | 459 | 759 | 1.9 | 5.4 | 65.532 |
| *Myxine glutinosa* (Hagfish) | | 3 | 417 | 494 | 4.0 | 5.2 | 64.527 |
| *Centroscyllium fabricii* (Black dogfish) | | 43 | 631 | 1 281 | 2.9 | 5.2 | 64.972 |
| *Somniosus microcephalus* (Greenland shark) | | 1 | 692 | 692 | 4.1 | 4.1 | 65.161 |
| *Bathyraja spinicauda* (Spinetail ray) | | 4 | 328 | 1 026 | 0.5 | 5.0 | 65.513 |
| *Amblyraja hyperborea* (Arctic skate) | | 14 | 312 | 1 460 | -0.6 | 3.4 | 71.612 |
| *Amblyraja radiate* (Starry skate) | | 20 | 291 | 906 | 0.1 | 5.1 | 70.597 |
| *Amblyraja fyllae* (Round ray) | | 7 | 328 | 910 | 1.1 | 5.3 | 66.212 |
| *Rajella bathyphila* (Deepwater ray) | | 2 | 869 | 1 460 | 1.1 | 3.4 | 65.392 |
| *Alepocephalus agassizzi* (Agassiz slickhead) | | 32 | 897 | 1 460 | 3.0 | 4.4 | 64.861 |
| *Alepocephalus bairdii* (Baird's smooth-head) | | 3 | 675 | 1 265 | 3.9 | 5.1 | 62.198 |
| *Bajacalifornia megalops* (Big-eye mooth-head) | | 1 | 391 | 873 | 0.5 | 3.2 | 65.536 |
| *Rouleina maderensis* (Maderian smooth-head) | p | 2 | 890 | 890 | 4.9 | 4.9 | 62.392 |
| *Xenodermichthys copei* (Bluntsnout smooth-head) | p | 2 | 316 | 1 257 | 2.2 | 5.6 | 65.536 |
| *Holtbyrnia anomala* (Bighead serasid) | p | 2 | 391 | 391 | 3.2 | 3.2 | 65.536 |
| *Maulisia mauli* (Maul's searasid) | p | 1 | 1 060 | 1 060 | 2.5 | 2.5 | 65.414 |
| *Maulisia microlepis* (Smallscale serasid) | p | 2 | 1 252 | 1 460 | 3.1 | 3.4 | 62.224 |
| *Normichthys operosus* (Multipore searsid) | | 1 | 1 072 | 1 072 | 3.0 | 3.0 | 64.861 |
| *Sagamichthys schnakenbecki* (Schnakenbeck's searsid) | p | 1 | 391 | 391 | 3.2 | 3.2 | 65.536 |
| *Cyclothone microdon* (Veiled anglemouth) | p | 37 | 316 | 1072 | 0.8 | 5.6 | 66.353 |
| *Polyipnus polli* (Poll's hatchetfish) | p | 2 | 316 | 444 | 5.0 | 5.6 | 62.436 |
| *Borostomias antarcticus* (Snaggletooth) | p | 5 | 391 | 1 460 | 2.4 | 4.0 | 65.551 |
| *Chauliodus sloani* (Sloane's viperfish) | p | 3 | 391 | 1 460 | 3.1 | 5.4 | 65.536 |
| *Stomias boa* (Boa dragonfish) | p | 6 | 316 | 1 281 | 2.0 | 5.6 | 65.551 |
| *Trigonolampa miriceps* (Threelight dragonfish) | p | 1 | 461 | 461 | 2.0 | 2.0 | 65.463 |
| *Malacosteus niger* (Stoplight loosejaw) | p | 1 | 873 | 1 252 | 0.5 | 3.1 | 65.355 |
| *Argentina silus* (Greater argentine) | p | 41 | 218 | 1 060 | 2.2 | 5.8 | 65.513 |
| *Nansenia groenlandica (*Greenland argentine) | p | 1 | 391 | 391 | 3.2 | 3.2 | 65.536 |
| *Bathylagus euryops* (Goiter blacksmelt) | p | 53 | 391 | 1 460 | 0.8 | 4.9 | 66.353 |
| *Mallotus villosus* (Capelin) | p | 27 8317 | 155 | 1 459 | -0.1 | 5.4 | 70.966 |
| *Scopelosaurus lepidus (*Blackfin wrayfish | p | 6 | 873 | 1 281 | 0.5 | 4.9 | 65.414 |
| *Benthosema glaciale* (Glacier lantern fish) | p | 1 069 | 316 | 896 | -0.2 | 5.6 | 71.067 |
| *Lampadena speculigera* (Mirror lanternfish) | p | 2 | 391 | 419 | 3.2 | 3.7 | 65.551 |
| *Lampanyctus intricarius* (Diamoncheek lanternfish) | p | 32 | 391 | 813 | 3.2 | 3.8 | 65.536 |
| *Lampanyctus macdonaldi* (Rakery beaconlamp) | p | 19 | 321 | 1 281 | 0.8 | 5.4 | 66.353 |
| *Myctophum punctatum* (Spotted lanternfish) | p | 31 | 164 | 1 265 | 1.1 | 5.6 | 66.212 |
| *Notoscopelus kroyeri* (Lancet fish) | | 9 | 316 | 1 460 | 1.1 | 5.6 | 65.478 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Protomyctophum arcticum (*Arctic telescope) | | 4 | 382 | 1 281 | 2.6 | 3.7 | 65.808 |
| *Arctozenus rissoi* (Spotted barracudina) | p | 6 | 462 | 910 | 0.8 | 5.2 | 66.353 |
| *Magnisudis atlantica* (Duckbill barracudina) | p | 51 | 419 | 1 281 | 1.1 | 4.9 | 65.551 |
| *Serrivomer beani* (Bean's sawtoothed eel) | p | 7 | 391 | 1 257 | 1.9 | 4.6 | 65.551 |
| *Nemichthys scolopaceus* (Slender snipe-eel) | p | 2 | 419 | 1 460 | 3.4 | 3.9 | 65.551 |
| *Synaphobranchus kaupi* (Kaup's arrowtooth eel) | | 58 | 631 | 1 460 | 2.3 | 5.2 | 65.399 |
| *Notacanthus chemnitzii* (Snubnosed spiny eel) | | 14 | 637 | 1 460 | 0.5 | 5.1 | 65.513 |
| *Gadomus longifilis* (Threadfin grenadier) | | 11 | 1 252 | 1 460 | 3.1 | 3.4 | 62.224 |
| Coryphaenoides güntheri (Günther's grenadier) | | 44 | 850 | 1 460 | 3.1 | 4.9 | 62.392 |
| *Coryphaenoides rupestris* (Roundnose grenadier) | | 300 | 410 | 1 460 | 0.5 | 5.1 | 65.414 |
| *Macrourus berglax* (Roughhead grenadier) | | 139 | 327 | 1 460 | 0.2 | 5.4 | 68.146 |
| *Nezumia bairdii* (Marlin-spike grenadier) | | 5 | 896 | 1 257 | 3.0 | 4.0 | 64.972 |
| *Trachyrhynchus murrayi* (Murray's longsnout grenadier) | | 31 | 850 | 1 281 | 3.0 | 5.0 | 64.861 |
| *Arctogadus glacialis* (Arctic cod) | p | 19 | 180 | 569 | 0.1 | 4.7 | 71.695 |
| *Boreogadus saida* (Polar cod) | p | 528 | 164 | 1 077 | -0.1 | 5.8 | 71.695 |
| *Gadus morhua* (Cod) | | 165 | 155 | 988 | 0.8 | 5.6 | 67.495 |
| *Melanogrammus aeglefinus* (Haddock) | | 262 | 155 | 464 | 0.8 | 5.4 | 66.353 |
| *Micromesistius poutassou* (Blue whiting) | p | 68 | 164 | 988 | 1.5 | 5.5 | 65.982 |
| *Pollachius virens* (Saith) | | 2 | 406 | 422 | 2.1 | 2.2 | 66.215 |
| *Trisopterus esmarki* (Norway pout) | | 8 | 236 | 426 | 5.1 | 5.4 | 62.216 |
| *Brosme brosme* (Torsk) | | 3 | 218 | 709 | 1.9 | 5.4 | 66.215 |
| *Gaidropsarus argentatus* (Arctic rockling) | | 21 | 289 | 1 459 | -0.6 | 5.3 | 71.612 |
| *Gaidropsarus ensis* (Threadfin rockling) | | 1 | 287 | 653 | 2.5 | 5.8 | 66.162 |
| *Molva dipterygia* (Blue ling) | | 19 | 218 | 890 | 1.5 | 5.4 | 65.877 |
| *Antimora rostrata* (Blue antimora) | | 38 | 850 | 1 460 | 3.0 | 5.0 | 64.972 |
| *Lepidion eques* (North Atlantic codling) | | 11 | 444 | 1 265 | 3.1 | 5.2 | 64.966 |
| *Hoplostethus atlanticus* (Orange roughy) | | 1 | 897 | 897 | 4.4 | 4.4 | 62.198 |
| *Poromitra capito* (Ridgehead) | p | 4 | 391 | 391 | 3.2 | 3.2 | 65.536 |
| *Scopeloberyx robustus* (Longjaw bigscale) | p | 1 | 1 072 | 1 072 | 3.0 | 3.0 | 64.861 |
| *Scopelogadus beanii* (Bean's bigscale) | p | 4 | 419 | 419 | 3.7 | 3.7 | 65.551 |
| *Chiasmodon niger* (Black swallower) | p | 1 | 890 | 890 | 4.9 | 4.9 | 62.392 |
| *Aphanopus carbo* (Black scabbard fish) | p | 1 | 391 | 1 072 | 2.9 | 5.1 | 65.536 |
| *Anarhichas denticulatus* (Jelly wolf-fish) | | 4 | 157 | 1 072 | 1.1 | 5.5 | 66.215 |
| *Anarhichas lupus* (Wolf-fish) | | 19 | 164 | 461 | 2.0 | 5.8 | 66.227 |
| *Anarhichas minor* (Spotted wolf-fish) | | 8 | 190 | 883 | 0.9 | 5.8 | 67.495 |
| *Leptoclinus maculatus* (Spotted snake blenny) | | 3 | 295 | 295 | 1.3 | 1.3 | 70.412 |
| *Lumpenus lampretaeformis* (Snake blenny) | | 1 | 316 | 316 | 5.6 | 5.6 | 62.436 |
| *Gymnelus retrodorsalis* (Aurora unernak) | | 1 | 287 | 377 | 2.5 | 2.8 | 66.162 |
| *Lycenchelys muraena* (Moray wolf eel) | | 1 | 1 260 | 1 260 | -0.5 | -0.5 | 71.612 |
| *Lycenchelys sarsi* (Sar's wolf eel) | | 1 | 417 | 431 | 4.1 | 4.1 | 64.527 |
| *Lycodes adolfi* (Adolf's eelpout) | | 5 | 676 | 1 341 | -0.3 | -0.2 | 71.249 |
| *Lycodes esmarki* (Greater eelpout) | | 2 | 416 | 692 | 1.1 | 4.1 | 67.899 |
| *Lycodes eudipleurostictus* (Doubleline eelpout) | | 10 | 351 | 1 088 | 0.2 | 2.1 | 70.597 |
| *Lycodes frigidus* (Glacial eelpout) | | 2 | 1 311 | 1 454 | -0.6 | -0.4 | 71.321 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Lycodes luetkenii (*Lütken's eelpout) | | 2 | 452 | 452 | 1.1 | 1.1 | 65.934 |
| *Lycodes paamiuti* (Paamiut eelpout) | | 5 | 459 | 1 343 | -0.5 | 5.4 | 71.612 |
| *Lycodes pallidus* (Pale eelpout) | | 6 | 295 | 1 123 | -0.3 | 1.3 | 71.249 |
| *Lycodes reticulatus* (Arctic eelpout) | | 6 | 291 | 546 | 0.1 | 3.8 | 70.597 |
| *Lycodes seminudus* (Longear eelpout) | | 7 | 381 | 1 125 | -0.2 | 1.3 | 71.067 |
| *Lycodes vahli* (Vahl's eelpout) | | 2 | 268 | 377 | 2.8 | 4.1 | 66.227 |
| *Lycodonus flagellicauda* ??? | | 2 | 1 260 | 1 260 | -0.5 | -0.5 | 71.612 |
| *Sebastes marinus* (Golden redfish) | | 373 | 155 | 1 257 | 0.5 | 5.8 | 67.478 |
| *Sebastes mentella* (Deep sea redfish) | | 4 011 | 155 | 1 460 | 0.5 | 5.8 | 66.365 |
| *Artediellus atlanticus* (Atlantic hookear sculpin) | | 10 | 118 | 1 077 | -1.2 | 2.8 | 71.692 |
| *Artediellus uncinatus* (Arctic hookear sculpin) | | 13 | 329 | 425 | 1.1 | 5.1 | 66.215 |
| *Icelus spatula* (Spatula sculpin) | | 1 | 328 | 328 | 4.2 | 4.2 | 64.471 |
| *Triglops murrayi* (Moustache sculpin) | | 13 | 164 | 988 | 1.1 | 5.4 | 67.478 |
| *Triglops nybelini* (Nybelin's sculpin) | | 96 | 118 | 1 077 | -1.2 | 2.5 | 71.695 |
| *Triglops pingeli* (Ribbed sculpin) | | 4 | 312 | 312 | 0.1 | 0.1 | 68.373 |
| *Cottunculus microps* (Polar sculpin) | | 22 | 118 | 1 260 | -1.2 | 5.1 | 71.612 |
| *Cottunculus thomsonii* (Pallid sculpin) | | 1 | 1 257 | 1 257 | 4.0 | 4.0 | 62.288 |
| *Leptagonus decagonus* (Atlantic poacher) | | 4 | 312 | 717 | 0.1 | 2.1 | 70.745 |
| *Cyclopterus lumpus* (Lumpsucker) | p | 1 | 157 | 157 | 5.2 | 5.2 | 64.427 |
| *Eumicrotremus spinosus* (Atlantic spiny lumpsucker) | | 1 | 295 | 459 | 1.0 | 1.3 | 70.412 |
| *Careproctus reinhardti* (Sea tadpole) | | 6 | 295 | 1 125 | -0.2 | 1.3 | 71.067 |
| *Liparis fabricii* (Gelatinous snailfish) | | 20 | 295 | 1 088 | -0.1 | 2.3 | 71.692 |
| *Liparis gibbus* (Variegated snailfish) | | 3 | 351 | 459 | 1.0 | 1.1 | 70.335 |
| *Paraliparis bathybius* (Black seasnail) | | 9 | 1 123 | 1 459 | -0.6 | 3.9 | 71.321 |
| *Paraliparis copei* (Blacksnout seasnail) | | 3 | 1 454 | 1 454 | 1.0 | 1.0 | 68.484 |
| *Rhodichthys regina* (Treadfin seasnail) | | 2 | 749 | 1 459 | -0.6 | 0.7 | 71.612 |
| *Glyptocephalus cynoglossus* (Witch) | | 6 | 328 | 811 | 4.1 | 4.2 | 65.161 |
| *Hippoglossoides platessoides* (Long rough dab) | | 50 | 164 | 988 | 0.5 | 5.8 | 71.695 |
| *Hippoglossus hippoglossus* (Halibut) | | 36 | 157 | 434 | 1.4 | 5.5 | 69.714 |
| *Reinhardtius hippoglossoides* Greenland halibut) | | 205 | 287 | 1 460 | -0.5 | 5.2 | 71.695 |
| *Lophius piscatorius* (Anglerfish) | | 1 | 631 | 631 | 5.2 | 5.2 | 62.297 |
| *Cryptopsaras couesii* (Triplewart seadevil) | p | 1 | 462 | 462 | 0.8 | 0.8 | 66.353 |

## Appendix 2

Primary species

| Cut off level | Level 1 | | Level 2 | | | Level 3 | | | | Level 4 | | | | Level 5 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Assemblage | 1,2,3 | 4–9 | 1,2,3 | 4,5 | 6–9 | 1 | 2,3 | 4,5 | 6–9 | 2,3 | 4,5 | 6,7 | 8,9 | 2 | 3 | 4,5 | 6,7 | 8,9 |
| *Centroscyllium fabricii* | 0.0 | 13.3 | 0.0 | **40.5** | 0.1 | 0.0 | 0.0 | 40.5 | 0.1 | 0.0 | 38.3 | 0.6 | 0.0 | 0.0 | 0.0 | 38.3 | 0.6 | 0.0 |
| *Amblyraja fyllae* | 0.0 | 19.4 | 0.0 | 2.8 | 17.0 | 0.0 | 0.0 | 2.8 | 17.0 | 0.0 | 1.4 | **44.1** | 0.0 | 0.0 | 0.0 | 1.4 | 44.1 | 0.0 |
| *Amblyraja hyperborea* | **62.4** | 0.0 | 61.4 | 0.1 | 0.0 | 56.3 | 14.8 | 0.0 | 0.0 | 14.8 | 0.0 | 0.0 | 0.0 | 7.3 | 21.5 | 0.0 | 0.0 | 0.0 |
| *Amblyraja radiata* | 10.8 | 9.1 | 8.5 | 2.6 | 8.9 | 0.0 | 18.0 | 2.1 | 7.0 | 12.7 | 1.5 | 17.8 | 0.5 | 13.3 | 3.2 | 1.2 | 14.3 | 0.4 |
| *Synaphobranchus kaupi* | 0.0 | 17.3 | 0.0 | 57.5 | 0.0 | 0.0 | 0.0 | 57.5 | 0.0 | 0.0 | 57.4 | 0.0 | 0.0 | 0.0 | 0.0 | 57.4 | 0.0 | 0.0 |
| *Notacanthus chemnitzii* | 0.0 | 16.3 | 0.0 | 61.5 | 0.0 | 0.0 | 0.0 | **61.5** | 0.0 | 0.0 | 61.5 | 0.0 | 0.0 | 0.0 | 0.0 | 61.5 | 0.0 | 0.0 |
| *Trachyrhynchus murrayi* | 0.0 | 7.1 | 0.0 | 26.9 | 0.0 | 0.0 | 0.0 | 26.9 | 0.0 | 0.0 | 26.9 | 0.0 | 0.0 | 0.0 | 0.0 | 26.9 | 0.0 | 0.0 |
| *Coryphaenoides rupestris* | 0.0 | 16.3 | 0.0 | 57.6 | 0.0 | 0.0 | 0.0 | 57.6 | 0.0 | 0.0 | 57.6 | 0.0 | 0.0 | 0.0 | 0.0 | 57.6 | 0.0 | 0.0 |
| *Macrourus berglax* | 0.7 | 48.5 | 0.2 | **91.3** | 2.4 | 0.1 | 0.3 | 89.8 | 2.3 | 0.3 | 84.4 | 2.1 | 1.8 | 0.0 | 1.7 | 82.2 | 2.1 | 1.8 |
| *Gadus morhua* | 0.0 | 45.9 | 0.0 | 0.0 | 62.4 | 0.0 | 0.0 | 0.0 | 62.4 | 0.0 | 0.0 | 5.2 | 71.5 | 0.0 | 0.0 | 0.0 | 5.2 | 71.4 |
| *Melanogrammus aeglefinus* | 0.0 | 23.5 | 0.0 | 0.0 | 31.9 | 0.0 | 0.0 | 0.0 | 31.9 | 0.0 | 0.0 | 0.0 | **51.1** | 0.0 | 0.0 | 0.0 | 0.0 | 51.1 |
| *Gaidropsarus argentatus* | 45.0 | 2.8 | 34.9 | 12.1 | 0.5 | **66.3** | 3.5 | 6.5 | 0.3 | 3.4 | 6.3 | 0.8 | 0.1 | 0.1 | 24.0 | 4.5 | 0.6 | 0.0 |
| *Molva dipterygia* | 0.0 | 26.5 | 0.0 | 10.1 | 15.6 | 0.0 | 0.0 | 10.1 | 15.6 | 0.0 | 5.9 | 37.3 | 0.5 | 0.0 | 0.0 | 5.9 | 37.3 | 0.5 |
| *Antimora rostrata* | 0.0 | 11.2 | 0.0 | 42.3 | 0.0 | 0.0 | 0.0 | 42.3 | 0.0 | 0.0 | 42.3 | 0.0 | 0.0 | 0.0 | 0.0 | 42.3 | 0.0 | 0.0 |
| *Lepidion eques* | 0.0 | 12.2 | 0.0 | 24.1 | 1.2 | 0.0 | 0.0 | 24.1 | 1.2 | 0.0 | 18.8 | 5.0 | 0.0 | 0.0 | 0.0 | 18.8 | 5.0 | 0.0 |
| *Anarhichas lupus* | 0.0 | 25.5 | 0.0 | 0.0 | 34.7 | 0.0 | 0.0 | 0.0 | 34.7 | 0.0 | 0.0 | 1.3 | 46.2 | 0.0 | 0.0 | 0.0 | 1.3 | 46.2 |
| *Sebastes mentella* | 0.0 | 75.5 | 0.0 | 1.5 | 78.6 | 0.0 | 0.0 | 1.5 | 78.6 | 0.0 | 0.7 | **96.4** | 1.7 | 0.0 | 0.0 | 0.7 | 96.4 | 1.7 |
| *Sebastes marinus* | 0.0 | 46.9 | 0.0 | 0.1 | 57.8 | 0.0 | 0.0 | 0.1 | 57.8 | 0.0 | 0.1 | 9.1 | 54.8 | 0.0 | 0.0 | 0.1 | 9.1 | 54.8 |
| *Artediellus atlanticus* | 33.9 | 0.1 | 33.4 | 0.0 | 0.1 | 0.0 | **56.1** | 0.0 | 0.1 | 54.7 | 0.0 | 0.0 | 0.3 | 52.4 | 5.2 | 0.0 | 0.0 | 0.2 |
| *Triglops murrayi* | 0.0 | 11.2 | 0.0 | 0.0 | 15.3 | 0.0 | 0.0 | 0.0 | 15.3 | 0.0 | 0.0 | 1.3 | **17.6** | 0.0 | 0.0 | 0.0 | 1.3 | 17.6 |
| *Triglops nybelini* | 40.7 | 0.0 | 40.5 | 0.0 | 0.0 | 0.0 | 67.1 | 0.0 | 0.0 | 66.6 | 0.0 | 0.0 | 0.1 | **90.2** | 0.0 | 0.0 | 0.0 | 0.1 |
| *Cottunculus microps* | 34.1 | 0.5 | 32.5 | 0.1 | 0.7 | 2.6 | 38.6 | 0.1 | 0.4 | 36.1 | 0.1 | 1.2 | 0.1 | 5.8 | **63.3** | 0.0 | 0.5 | 0.0 |
| *Liparis fabricii* | 47.1 | 0.0 | 47.1 | 0.0 | 0.0 | 3.3 | 53.2 | 0.0 | 0.0 | 53.2 | 0.0 | 0.0 | 0.0 | **74.2** | 0.0 | 0.0 | 0.0 | 0.0 |
| *Hippoglossoides platessoides* | 0.5 | 32.9 | 0.4 | 0.0 | **45.4** | 0.0 | 1.0 | 0.0 | 44.3 | 0.5 | 0.0 | 8.6 | 41.0 | 1.0 | 0.0 | 0.0 | 8.5 | 40.5 |
| *Reinhardtius hippoglossoides* | 16.2 | 37.9 | 6.1 | **76.6** | 2.5 | 0.0 | 13.6 | 71.6 | 2.3 | 12.7 | 66.8 | 6.4 | 0.4 | 9.0 | 15.7 | 56.0 | 5.3 | 0.3 |

Primary species cont.

| Cut off level | Level 6 | | | | Level 7 | | | Level 8 | |
|---|---|---|---|---|---|---|---|---|---|
| Assemblage | 4,5 | 6,7 | 8 | 9 | 4 | 5 | 6,7 | 6 | 7 |
| *Centroscyllium fabricii* | 38.3 | 0.6 | 0.0 | 0.0 | 27.4 | 15.4 | 0.3 | 0.0 | 1.0 |
| *Amblyraja fyllae* | 1.4 | 44.1 | 0.0 | 0.0 | 0.7 | 1.6 | 40.6 | 23.3 | 19.6 |
| *Amblyraja hyperborea* | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Amblyraja radiata* | 1.2 | 14.0 | 0.0 | 0.8 | 0.4 | 1.8 | 13.3 | 1.2 | **24.2** |
| *Synaphobranchus kaupi* | 57.4 | 0.0 | 0.0 | 0.0 | **95.7** | 1.3 | 0.0 | 0.0 | 0.0 |
| *Notacanthus chemnitzii* | 61.5 | 0.0 | 0.0 | 0.0 | 9.3 | 56.0 | 0.0 | 0.0 | 0.0 |
| *Trachyrhynchus murrayi* | 26.9 | 0.0 | 0.0 | 0.0 | **70.0** | 0.0 | 0.0 | 0.0 | 0.0 |
| *Coryphaenoides rupestris* | 57.6 | 0.0 | 0.0 | 0.0 | **97.2** | 0.9 | 0.0 | 0.0 | 0.0 |
| *Macrourus berglax* | 79.8 | 2.0 | 0.0 | 3.2 | 39.6 | 48.9 | 1.2 | 0.3 | 2.2 |
| *Gadus morhua* | 0.0 | 2.1 | **73.8** | 15.6 | 0.0 | 0.0 | 2.1 | 7.5 | 0.0 |
| *Melanogrammus aeglefinus* | 0.0 | 0.0 | 5.8 | 44.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Gaidropsarus argentatus* | 4.4 | 0.6 | 0.1 | 0.0 | 0.4 | 8.2 | 0.5 | 0.5 | 0.5 |
| *Molva dipterygia* | 5.8 | 36.4 | 0.0 | 0.8 | 9.0 | 2.3 | 27.9 | **50.3** | 1.9 |
| *Antimora rostrata* | 42.3 | 0.0 | 0.0 | 0.0 | **99.6** | 0.0 | 0.0 | 0.0 | 0.0 |
| *Lepidion eques* | 18.8 | 5.0 | 0.0 | 0.0 | **25.7** | 4.2 | 3.1 | 0.0 | 8.5 |
| *Anarhichas lupus* | 0.0 | 0.6 | 18.7 | 24.7 | 0.0 | 0.0 | 0.6 | 2.9 | 0.0 |
| *Sebastes mentella* | 0.7 | 95.5 | 0.0 | 3.1 | 0.0 | 1.5 | 94.9 | 90.0 | 7.6 |
| *Sebastes marinus* | 0.1 | 7.0 | 2.8 | **64.8** | 0.1 | 0.0 | 7.0 | 20.5 | 0.0 |
| *Artediellus atlanticus* | 0.0 | 0.0 | 0.6 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Triglops murrayi* | 0.0 | 0.8 | 13.8 | 8.4 | 0.0 | 0.0 | 0.8 | 1.3 | 0.2 |
| *Triglops nybelini* | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Cottunculus microps* | 0.0 | 0.5 | 0.0 | 0.1 | 0.0 | 0.1 | 0.5 | 0.3 | 0.6 |
| *Liparis fabricii* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Hippoglossoides platessoides* | 0.0 | 5.8 | 12.5 | 33.6 | 0.0 | 0.0 | 5.8 | 11.4 | 1.2 |
| *Reinhardtius hippoglossoides* | 55.7 | 5.3 | 0.0 | 0.6 | 73.2 | 5.2 | 2.8 | 0.1 | 7.3 |

Secondary species

| Cut off level | Level 1 | | Level 2 | | | Level 3 | | | | Level 4 | | | | Level 5 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Assemblage | 1,2,3 | 4–9 | 1,23, | 45, | 6 –9 | 1 | 2,3 | 4,5 | 6–9 | 2,3 | 4,5 | 6,7 | 8,9 | 2 | 3 | 4,5 | 6,7 | 8,9 |
| *Bathyraja spinicauda* | 0.0 | 13.3 | 0.0 | **30.3** | 0.7 | 0.0 | 0.0 | 30.3 | 0.7 | 0.0 | 26.0 | 3.2 | 0.0 | 0.0 | 0.0 | 26.0 | 3.2 | 0.0 |
| *Brosme brosme* | 0.0 | **16.3** | 0.0 | 4.1 | 11.7 | 0.0 | 0.0 | 4.1 | 11.7 | 0.0 | 2.3 | 13.7 | 2.8 | 0.0 | 0.0 | 2.3 | 13.7 | 2.8 |
| *Anarhichas denticulatus* | 0.0 | **25.5** | 0.0 | 12.1 | 12.5 | 0.0 | 0.0 | 12.1 | 12.5 | 0.0 | 8.0 | 14.9 | 4.5 | 0.0 | 0.0 | 8.0 | 14.9 | 4.5 |
| *Anarhichas minor* | 0.7 | 14.5 | 0.5 | 0.5 | **16.5** | 0.0 | 1.2 | 0.5 | 15.4 | 0.7 | 0.3 | 3.7 | 15.6 | 0.0 | 8.1 | 0.2 | 2.8 | 11.8 |
| *Lycodes eudipleurostictus* | **21.2** | 1.4 | 18.0 | 0.5 | 1.5 | 10.7 | 8.6 | 0.3 | 0.8 | 7.6 | 0.3 | 1.3 | 0.4 | 10.4 | 0.7 | 0.2 | 1.1 | 0.4 |
| *Lycodes paamiuti* | 8.3 | 0.3 | 6.9 | 0.8 | 0.1 | **15.6** | 0.2 | 0.4 | 0.1 | 0.2 | 0.4 | 0.0 | 0.2 | 0.0 | 2.8 | 0.3 | 0.0 | 0.2 |
| *Lycodes pallidus* | **15.5** | 0.9 | 14.1 | 0.0 | 1.4 | 6.0 | 10.0 | 0.0 | 0.9 | 8.3 | 0.0 | 1.1 | 0.4 | 10.4 | 1.0 | 0.0 | 0.9 | 0.4 |
| *Lycodes reticulatus* | 21.2 | 0.0 | 21.0 | 0.0 | 0.0 | 0.0 | **34.9** | 0.0 | 0.0 | 34.5 | 0.0 | 0.0 | 0.1 | 16.8 | 13.9 | 0.0 | 0.0 | 0.0 |
| *Lycodes seminudus* | **12.2** | 0.7 | 11.2 | 0.0 | 1.2 | 5.4 | 7.6 | 0.0 | 0.7 | 6.4 | 0.0 | 1.1 | 0.3 | 2.9 | 5.9 | 0.0 | 0.6 | 0.2 |
| *Leptagonus decagonus* | 18.4 | 0.1 | 18.0 | 0.0 | 0.2 | 0.0 | 30.6 | 0.0 | 0.1 | 29.0 | 0.0 | 0.2 | 0.1 | **40.1** | 0.0 | 0.0 | 0.1 | 0.1 |
| *Careproctus reinhardti* | **33.3** | 0.0 | 33.3 | 0.0 | 0.0 | 24.8 | 11.0 | 0.0 | 0.0 | 11.0 | 0.0 | 0.0 | 0.0 | 4.8 | 15.6 | 0.0 | 0.0 | 0.0 |
| *Paraliparis bathybius* | 13.3 | 0.0 | 12.4 | 0.4 | 0.0 | **33.6** | 0.0 | 0.2 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 |
| *Rhodichthys regina* | 17.6 | 0.0 | 17.6 | 0.0 | 0.0 | **24.8** | 1.9 | 0.0 | 0.0 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 | 15.3 | 0.0 | 0.0 | 0.0 |

| Cut off level | Level 6 | | | | Level 7 | | | Level 8 | |
|---|---|---|---|---|---|---|---|---|---|
| Assemblage | 4,5 | 6,7 | 8 | 9 | 4 | 5 | 6,7 | 6 | 7 |
| *Bathyraja spinicauda* | 26.0 | 3.2 | 0.0 | 0.0 | 3.5 | 29.1 | 2.0 | 2.8 | 1.0 |
| *Brosme brosme* | 2.2 | 12.8 | 0.0 | 4.9 | 0.0 | 5.2 | 11.4 | 14.3 | 3.2 |
| *Anarhichas denticulatus* | 7.0 | 12.9 | 0.8 | 5.7 | 5.2 | 5.3 | 9.8 | 8.5 | 5.9 |
| *Anarhichas minor* | 0.2 | 2.1 | 5.4 | 10.2 | 1.1 | 0.0 | 1.9 | 6.1 | 0.1 |
| *Lycodes eudipleurostictus* | 0.2 | 1.1 | 0.0 | 0.7 | 0.0 | 0.6 | 1.1 | 0.0 | 3.2 |
| *Lycodes paamiuti* | 0.3 | 0.0 | 0.0 | 0.3 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 |
| *Lycodes pallidus* | 0.0 | 0.9 | 0.0 | 0.7 | 0.0 | 0.0 | 0.9 | 0.0 | 2.6 |
| *Lycodes reticulatus* | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Lycodes seminudus* | 0.0 | 0.6 | 0.0 | 0.3 | 0.0 | 0.0 | 0.6 | 0.0 | 1.9 |
| *Leptagonus decagonus* | 0.0 | 0.1 | 0.0 | 0.2 | 0.0 | 0.0 | 0.1 | 0.0 | 0.4 |
| *Careproctus reinhardti* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Paraliparis bathybius* | 0.2 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Rhodichthys regina* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

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# Atlantic herring (*Clupea harengus*) demographics in the Gulf of Maine from 1998 to 2012

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## Abstract

Atlantic herring (*Clupea harengus*) in the Georges Bank, Gulf of Maine, and southern New England regions were sampled from early September into mid-November by the Northeast Fisheries Science Center during their annual randomly-stratified bottom trawl and systematic acoustic/midwater trawl surveys. Atlantic herring were randomly selected for length distributions and systematically subsampled for biological metrics (*e.g.*, weight, age, maturity, and sex). Broad similarities in Atlantic herring biological metrics between midwater and bottom trawl catches suggest both gear types provide comparable sampling of herring demographics in the Gulf of Maine and Georges Bank regions during autumn. Annual mean lengths and weights and temporal patterns of herring size were consistently similar between gear types. Similarity in age structure between Georges Bank and the Gulf of Maine suggest a similar response to intrinsic and extrinsic factors between herring stocks in these regions, but apparent asynchrony in spawning timing suggests some level of independence between these stocks. Overall similarities can mask interesting distinctions such as midwater trawls seem to sample younger, smaller, but heavier fish than do bottom trawls. Sampling of historical spawning sites appears to characterize the biological state of Atlantic herring in the Georges Bank region and could be utilized to design an efficient sampling scheme for Atlantic herring in the Gulf of Maine.

*Keywords*: Atlantic herring, biological metrics, Gulf of Maine, Georges Bank, midwater trawl, bottom trawl

## Introduction

Ontogenetic changes in pelagic and semi-pelagic fish species are often reflected in their vertical distribution. In some species, such as walleye pollock (*Theragra chalcogramma*), younger fish are predominantly found in the water column and older fish tend to the bottom (Honkalehto *et al.*, 2011). In other species, such as lake herring (*Coregonus artedi*), juveniles tend to the bottom and adults are predominantly found in the water column (Stockwell *et al.*, 2006). These changes, as well as diel vertical migration and cross-bathymetry movement, can have implications for survey design and selection of sampling gear (*e.g.*, Pillar and Barange, 1997; Stockwell *et al.*, 2007; Yule *et al.*, 2007), especially when only one type of gear is employed during a survey. Integrating numerous gear types that appropriately sample the biological organisms and physical habitat is an ideal approach to estimate "absolute" biomass and abundance (Yule *et al.*, 2007; Stockwell *et al.*, 2007) when relative trends are not sufficient for management needs (Yule *et al.*, 2009). Yet the logistics of sampling with multiple gear types often precludes certain vessel types and often requires more personnel to process the samples than available berths. For example, a fishing vessel requires two net reels and the capability to quickly swap nets and doors to conduct sequential trawl operations. But not properly sampling the living resources can result in substantial (*e.g.*, order of magnitude) differences in biomass estimates among bottom trawl, midwater trawl, and acoustic data, and time of sampling (day vs. night) for schooling, pelagic species (Yule *et al.*, 2007).

Atlantic herring (*Clupea harengus*) in the Gulf of Maine, Georges Bank, and southern New England regions have been sampled from early September into November by the Northeast Fisheries Science Center during their annual stratified-random bottom trawl survey (Politis *et al.*, 2014) and dedicated systematic acoustic/midwater trawl survey of Atlantic herring (Overholtz *et al.*, 2006). The dedicated herring survey was an acoustic and midwater trawl survey designed to systematically sample prespawning aggregations of herring in the Georges Bank and Great South Channel area of southern Gulf of Maine as well as historical spawning sites in the Gulf of Maine. This survey was conducted annually from 1998 to 2012 covering approximately the same areas during late September into mid October (Jech and Stroman, 2012). This survey was established to determine if a dedicated herring survey could provide age-based abundance measures (Jech and Sullivan, 2014) for stock assessments. The bottom trawl survey is a stratified-random design, multi-species survey that begins near Cape Hatteras, NC in early September and enters the Gulf of Maine in mid to late October (Azarovitz *et al.*, 1997). It is the primary fisheries-independent survey conducted in the Northeast United States for stock assessment purposes (Anonymous, 2012).

The systematic and stratified-random surveys are independent of each other and currently trawl data collected during these surveys have been analyzed independently. However, the spatial and temporal extents of sampling Atlantic herring can be expanded by combining the data collected by those surveys (Fig. 1) (Jech and Sullivan, 2014) which might offer some advantages. However, the sampling strategies, the vertical location of the net during sampling (*i.e.*, altitude of the net), and the physiological and behavioral changes in herring over their spawning season may complicate a common analysis. Our goals are to compare the biological samples collected by both surveys to evaluate similarities or differences in measurements of herring demographics, and ultimately to assess whether the data can be used independently or combined into one comprehensive data set.

## Materials and Methods

Analyses in this paper will focus on Atlantic herring data collected from bottom and midwater trawls in the Georges Bank (GB), Gulf of Maine (GoM), and southern New England (SNE) regions during the autumn season from 1998 to 2012. Temporally, trawl catches were compared from 1998 to 2012, which are years with both midwater and bottom trawl hauls in Gulf of Maine, Georges Bank, and southern New England. Spatially, trawl catches were segregated into the GB, GoM, and SNE analysis areas (Fig. 1; Jech and Sullivan, 2014). Data analyses were done in R statistical software (R Core Team, 2015), the PBSmapping R package (Schnute *et al.*, 2004), 'aov' in the R stats package (v3.3.0), and QGIS (QGIS Development Team, 2014). The Georges Bank area was defined as 40 nautical miles (nmi) north and 10 nmi south of the 90 m bathymetric contour, the far eastern end of Georges Bank, and Cape Cod to the west, and encompasses the majority of the systematic herring surveys on Georges Bank (Jech and Stroman, 2012). The Gulf of Maine area is bounded to the south by the Georges Bank analysis area and Cape Cod, and the other boundaries are set to include all trawl hauls north of the Georges Bank area. The southern New England area was bounded to the north by the southern boundary of the GB area, and bounded to the south by the southernmost trawl catch with Atlantic herring present.

### Midwater Trawl

Midwater trawl (MWT) hauls were conducted during the systematic Atlantic herring acoustic surveys to collect

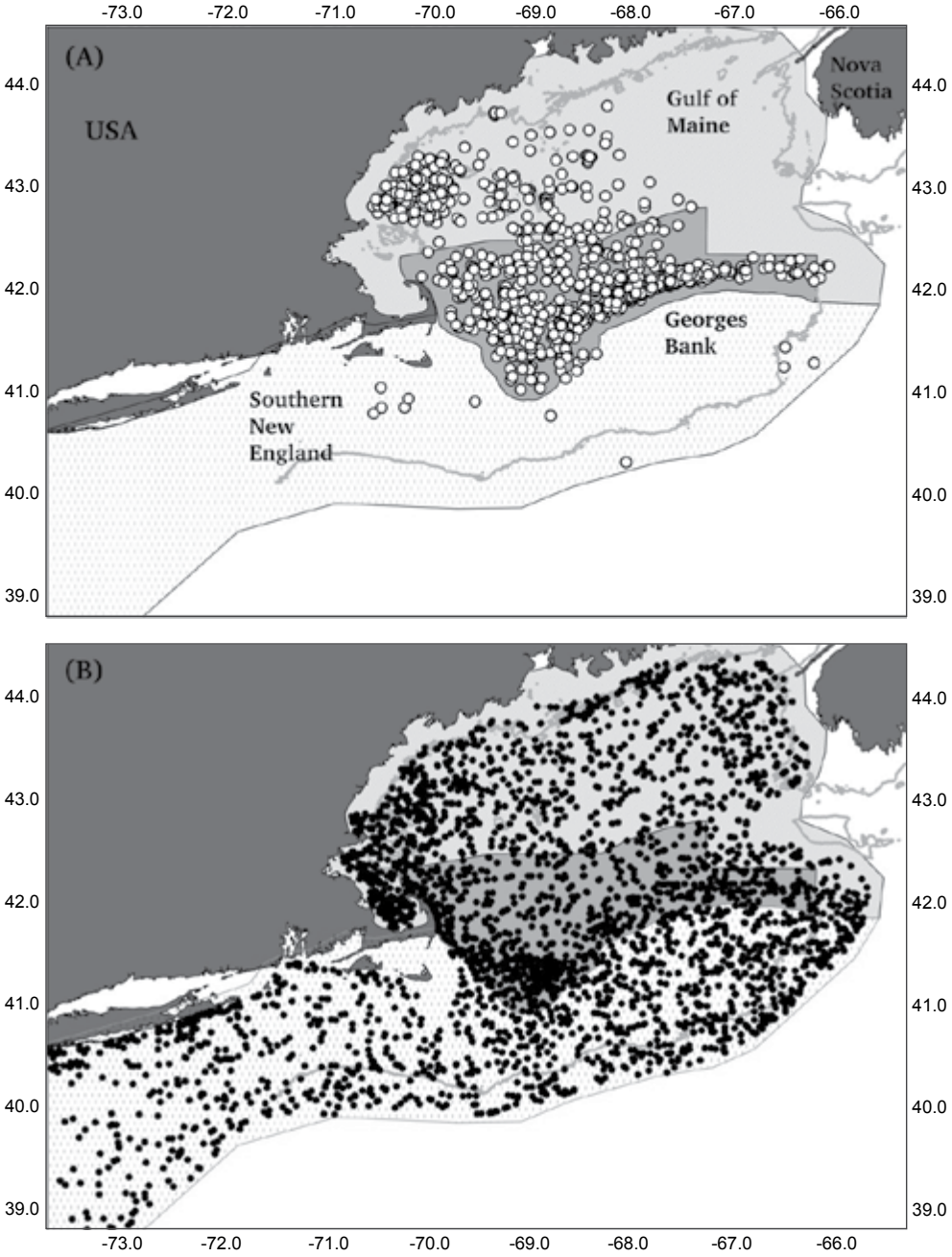


Fig. 1. Midwater trawl (**A**) and bottom trawl (**B**) locations from 1998 to 2012 and analysis areas (Georges Bank is the medium gray area) for spatially aggregating the trawl data.

biological samples. The primary survey was designed to estimate abundance of prespawning herring in the Georges Bank region (Overholtz *et al.*, 2006; Jech & Sullivan, 2014). The systematic survey design was composed of parallel-transects oriented north-south along Georges Bank, and targeted midwater trawl hauls that varied in duration and depth to identify the species composition of acoustic backscatter and to collect Atlantic herring. Systematic survey operations also included historical spawning sites in the Gulf of Maine, such as Jeffreys, Cashes, and Fippennies Ledges, and Platts Bank. The surveys were conducted in the Georges Bank region from mid to late September into early October, and in the Gulf Maine areas from early to mid October, with the exception of 2007 when the survey was conducted in mid to late October (Jech & Sullivan, 2014). Data were collected from the NOAA Ship Fisheries Research Vessel (FRV) *Delaware II* (hereafter DE II) from 1998–2011 and

the NOAA Ship Fisheries Survey Vessel (FSV) *Pisces* (hereafter *PC*) in 2012 (Fig. 2).

A High Speed Midwater Rope Trawl (Gourock Trawls, Ferndale, WA, USA) was used from 1998–2006 (Jech and Michaels, 2006); an Irish Herring Midwater Trawl (Swan Net-Gundry, Gloucester, MA, USA) was used from 2007–2010; and a Polytron Midwater Rope Trawl (Superior Net, Pt. Judith, RI, USA) was used from 2011–2012 (Fig. 2). All midwater trawls adhered to a rope trawl design (Dotson and Griffith, 2006) with nearly identical mouth openings of approximately 15 m vertical by 30-m horizontal (Jech and Sullivan, 2014). Mesh sizes ranged from 6.5 m near the mouth to 5.1 cm stretch mesh near the cod end. The cod-end liner was 0.635-cm stretch (hexagonal mesh shape) knotless nylon.

Catches were sorted, total weights by species recorded, and length distributions were measured for each species according to NEFSC trawl survey protocols (Azarovitz *et al.*, 1997; Politis *et al.*, 2014). Biological sampling (see Biological Sampling section) was concentrated on Atlantic herring. Trawls were categorized into day, night, dawn, and dusk based on sunrise, sunset, and nautical twilight (Jech and Stroman, 2012). Data, including latitude, longitude, and time (Greenwich Mean Time, GMT) of each trawl, were entered into the Fisheries Scientific Computing System (FSCS) and digitally recorded into the FSCS database. Digital time-depth recorders (Vemco Ltd., Bedford, Nova Scotia, CA) attached to the headrope and footrope of each trawl provided trawl performance and tow profile data which were downloaded after each trawl haul to a laptop computer and then transferred into a relational database table.

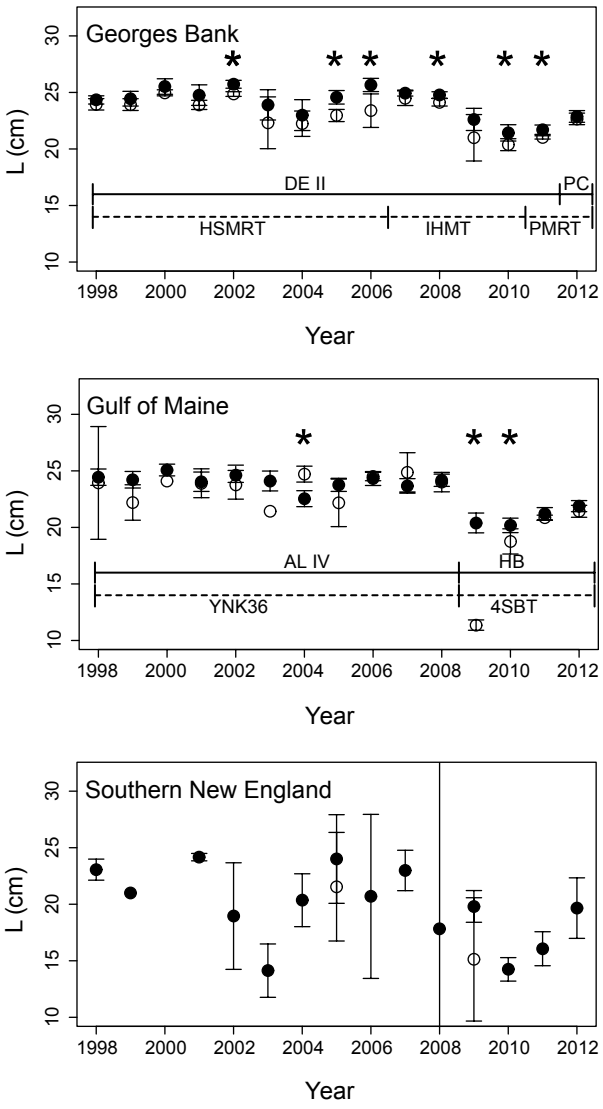


Fig. 2. Annual Atlantic herring mean length (L (cm)) in the Georges Bank (top panel), Gulf of Maine (middle panel), and southern New England (bottom panel) analysis areas for midwater trawl (open circles) and bottom trawl (solid circles) catches. Error bars are 95% confidence interval. Points with no error bars denote years where only one trawl occurred in that area. Asterisks denote years where the mean lengths were not statistically equivalent at the 5% level. Timelines for each vessel and gear type are presented. "DE" denotes the NOAA Ship *Delaware II*, "PC" denotes the NOAA Ship *Pisces*, "AL IV" denotes the NOAA Ship *Albatross IV*, and "HB" denotes the NOAA Ship *Henry Bigelow*. "HSMRT" denotes the high-speed midwater rope trawl, "IHMT" denotes the Irish herring midwater trawl, "PMRT" denotes the polytron midwater rope trawl, "YNK36" denotes the Yankee 36 bottom trawl, and "4SBT" denotes the 4-seam bottom trawl.

**Bottom Trawl**

Bottom-trawl (BT) hauls were conducted at predetermined stations randomly selected within strata throughout the survey area from Cape Hatteras, NC in early September and progressed northward along the continental shelf to Georges Bank and the Gulf of Maine in mid-October. The GB, GoM, and SNE regions were sampled from mid-October to mid-November (Jech and Sullivan, 2014). The stratified-random survey design allocates effort based on bathymetrically-defined strata where bottom trawl locations are selected randomly within each stratum prior to the survey commencing (Politis *et al.*, 2014). However, sampling order is not random and is determined by minimizing travel time between trawl locations. Data were collected aboard the NOAA Ship FRV *Albatross* (hereafter *AL IV*) from 1998–2008, and aboard the NOAA Ship FSV *Henry B Bigelow* (hereafter *HB*) from 2007–2012. In

2007–2008, data were collected from both vessels in an effort to compare species catch distributions (*i.e.*, calibrate) between ships (Miller *et al.*, 2010). For these analyses, BT data from the *AL IV* during 1998–2008 and from the *HB* during 2009–2012 (Fig. 2) were used because the spatial coverage of the *HB* during 2007–2008 was limited.

A Yankee 36 bottom trawl (Azarovitz *et al.*, 1997) was used from the 1960s until 2007 aboard the *AL IV* (Fig. 2). The net had a 2 m vertical by 10 m horizontal mouth opening and was towed at 3.8 knots for 30 minutes, sweeping an area of approximately 0.0352 km$^2$ (Jech and Sullivan, 2014). From 2008-present aboard the *HB* a four-seam bottom trawl system (Politis *et al.*, 2014) was used with a 5 m vertical by 13 m horizontal mouth opening. This system was towed at 3 knots for 20 minutes, sweeping approximately 0.024 km$^2$ (Jech and Sullivan, 2014). The trawl catches were sorted to species, total weight for each species recorded, and comprehensive sampling and sub-sampling protocols were followed for all species (Wigley *et al.*, 2003). Latitudes, longitudes, and GMT time were also recorded for each trawl location, as well as the seafloor depth (used as a proxy for the trawl depth), and duration of each trawl was standardized to 30 minutes for the Yankee 36 and 20 minutes for the four-seam trawls. Trawl and biological data were recorded at sea into the FSCS database and audited on shore.

During the Atlantic herring acoustic/midwater trawl survey in 2012 on the *PC*, bottom trawl hauls were conducted opportunistically and in conjunction with midwater trawl hauls in selected sites to begin investigating catches of Atlantic herring between the two gear types (Fig. 3). Midwater (PMRT) trawl deployments were conducted and catches were processed as per standard procedures. Bottom trawl (4SBT) deployments were conducted and catches were processed as per standard procedures, except that tow duration was 10 min. rather than the standard 20 minutes. The shorter duration was due primarily to limited number of personnel on board to efficiently process the catch. At selected sites (clusters of trawl locations in Fig. 3), eight trawl hauls were conducted over a 24-hour period, with two PMRT and two 4SBT trawl hauls during day and two of each at night. The configuration of the *PC* with two net reels and ability to swap door connections within 10 minutes, allowed sequential trawling between gear types. Mean lengths per trawl haul were calculated from the length frequency distribution and were

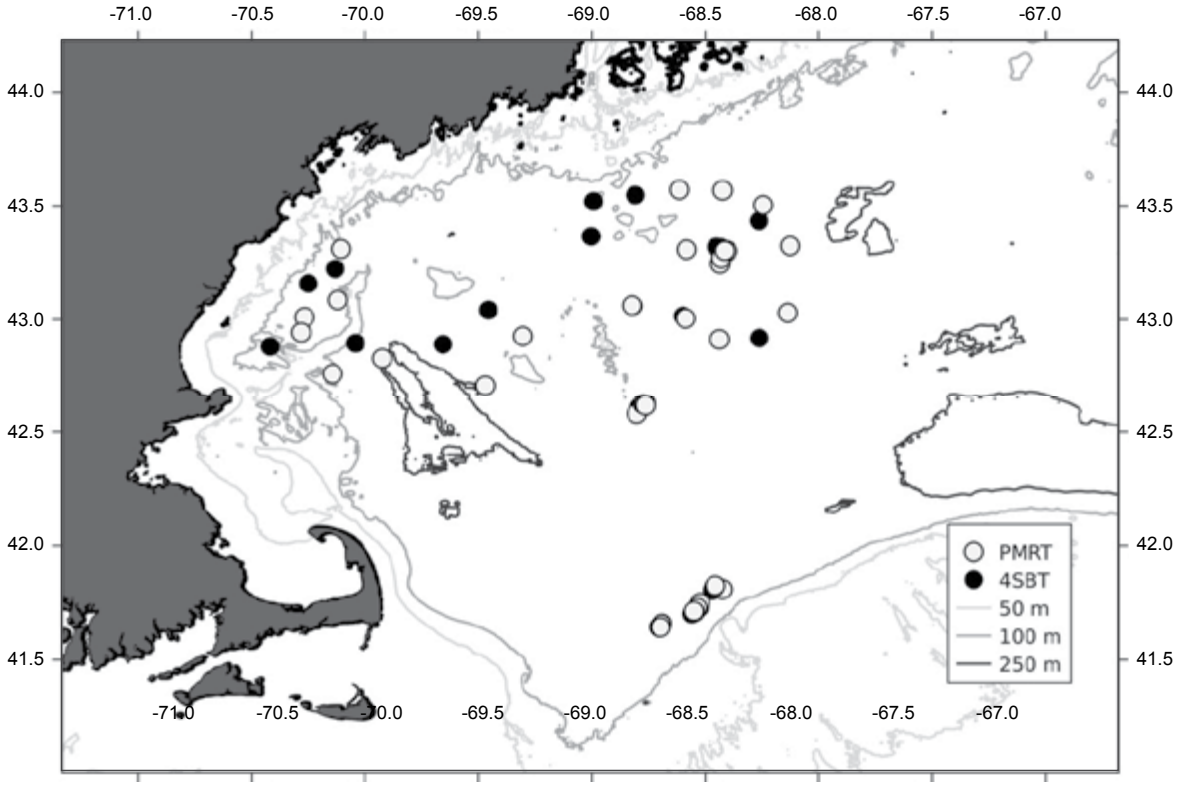


Fig. 3. Polytron midwater rope trawl (PMRT, open circles) and four-seam bottom trawl (4SBT, solid circles) locations during the 2012 Atlantic herring acoustic/midwater trawl survey on the NOAA Ship *Pisces*.

categorized as day or night (Jech and Stroman, 2012) and by gear type (PMRT or 4SBT).

**Biological Subsampling**

For both the midwater and bottom trawl surveys, up to approximately 150 Atlantic herring individuals were randomly selected (randomly-selected Atlantic herring) from each catch and individual fork length (FL) measurements were collected for all these individuals. Fork lengths from midwater trawl catches were measured to the nearest millimeter using Ichthystick electronic measuring boards (built in-house at the NEFSC) and recorded in the FSCS database with 0.1 cm precision, whereas fork lengths from bottom-trawl catches were measured to the nearest 0.5 cm using Scantrol (Scantrol AS, Bergen, NO) electronic measuring boards and then recorded in the FSCS database to the nearest integer centimeter (Price *et al.*, 2015). Differences in length measurement instrumentation and procedures between survey types were independently evaluated and did not result in significant differences in mean lengths (Price *et al.*, 2015). Length measurements were scaled by the total catch of Atlantic herring to generate length-frequency distributions that were representative of the local assemblage of herring. In addition, the weight of each randomly selected individual in midwater trawl catches was measured. From the random selections, individuals were systematically subsampled for biological measurements.

Subsamples of the randomly selected individuals were systematically sampled based on length (systematic subsampling or length-stratified subsampling (Morgan and Hoenig, 1997)). As a general rule for midwater and bottom trawl catches, the first individual measured in each 1 cm length interval below 25 cm FL was collected. Pre-2002, one individual per 1 cm length interval for all lengths was collected. Beginning in 2002, the Atlantic herring stock assessment recommended collecting a greater proportion of otolith samples for age estimation from larger herring – *i.e.*, more individuals per length interval above a prescribed FL. For midwater trawl catch processing, three individuals per 1 cm length interval greater than or equal (≥) to 25 cm were collected for biological subsampling. This protocol remained constant for the midwater trawl catches through 2012. Beginning in 2002 for the bottom-trawl catches, at least five individuals per 1 cm length interval ≥ 25 cm were collected for biological subsampling and during some years all herring ≥ 30 cm were retained.

For the subsampled individuals the weight measurements of the intact individual to the nearest 1 g were collected using Marel scales (Marel, Gardabaer, Iceland), as well as other biological measurements such as sex determination, maturity staging, evaluation of stomach contents, and otolith collection. In addition, for the midwater trawl catches during 2010–2012 the gonad weights (gonads extracted and weighed alone) to the nearest 1 g from were recorded.

Stomach contents were sampled according to NEFSC protocols (Link and Almeida, 2000; Smith and Link, 2010). Otoliths were collected by tagging and freezing the individual for extraction at the NEFSC at a later date. Sex was determined by visual examination of the gonads. In the case of immature individuals, every attempt was made to determine sex, but when sex was indistinguishable, the individual was categorized as "unknown". Maturity stages were categorized as unknown (code "X"), immature (code "I"), developing (code "D"), ripe (code "R"), ripe and running (code "U"), spent (code "S"), and resting (code "T"). In this paper, we define herring in prespawning condition as developing (D), in spawning condition as ripe and ripe and running (R and U), and in non-spawning or postspawned condition as spent and resting (S and T) (Bucholtz *et al.*, 2008).

In summary, each midwater trawl catch has approximately 150 randomly-selected individual length and weight measurements, and each bottom-trawl catch has approximately 150 randomly-selected individual length measurements. Both surveys have biological subsamples for each trawl catch selected systematically (*i.e.*, length stratified) as one individual per 1 cm length interval less than 25 cm. For individuals 25 cm and longer, each midwater trawl catch has biological measurements for one to three individuals per 1-cm length interval, and each bottom trawl catch has biological measurements for one to all individuals per 1 cm length interval.

**Data Analyses**

Mean length for each trawl haul was calculated from the length distribution generated from the ~150 randomly-selected individuals, and the station means were used to calculate the mean length and 95% confidence interval (CI) for each area and time period. Each trawl haul was treated as an independent and representative sample of Atlantic herring at the time and location of the trawl haul, and length distributions were not pooled among trawl hauls. Bottom trawl hauls were standardized for duration whereas midwater trawl hauls were not, thus pooling length distributions among midwater trawl catches can be problematic when the magnitude of the catch is not representative of the abundance. Annual means were calculated for each area. Mean lengths for each area were calculated at approximately weekly intervals – four intervals per month – from the beginning of September to the beginning of December.

The uneven length-stratified subsampling potentially affects summary statistics of biological subsamples (*e.g.*, Morgan and Hoenig, 1997; Morgan, 1999). For example, because larger individuals were sampled more intensively, a simple mean of ages will potentially be biased towards older ages. To account for the uneven subsampling, maturity, age, and weight (of biological subsamples) were scaled by the length distribution for each midwater and bottom trawl catch and then compared to means using all individuals within the subsamples. Scaling by the length distribution assumes the length distribution is representative of the herring assemblage and that the biological variables are scalable by length.

The maturity stages are discrete categories that describe conditions within an annual cycle rather than over a lifetime. The scaled proportion for each maturity stage was calculated by scaling the proportion of individuals within the biological subsample in each maturity stage by the length distribution from each trawl haul:

$$nM_m = \sum_{l=1}^{nLF} \left[ \frac{n(M_m, FL_l)}{n(FL_l)} * n(LF_l) \right], \qquad (1)$$

where $nM_m$ is the number of individuals at the $m^{th}$ maturity stage ($M$) scaled for oversampling at larger length intervals, $l$ indexes length, $n(LF_l)$ is the number of individuals at the $l^{th}$ length interval, $n(M_m, FL_l)$ is the number of individuals of the $m^{th}$ maturity stage at the $l^{th}$ FL from the subsample, and $n(FL_l)$ is the total number of Atlantic herring individuals biologically subsampled at the $l^{th}$ FL (sensu Morgan and Hoenig, 1997). There were 40 length intervals ($n(LF)$, 1 to 40 cm) and 6 maturity stages. The unknown maturity category ("X") was excluded from analysis to be consistent with the bottom trawl survey which seldom used the code (48 occurrences of more than 10 600 individuals measured), and the herring assessment (NEFSC, 2012). $nM_m$ is divided by the total number of individuals in the length frequency distribution ($N_T$) for the proportion of each maturity stage in each trawl haul ($PM_m$)

$$N_T = \sum_{l=1}^{nLF} n(LF_l), \qquad (2)$$

$$PM_m = \frac{nM_m}{N_T}. \qquad (3)$$

The mean length scaled proportion for each maturity stage was computed for all trawls in an analysis area and time interval.

Age estimates are given as discrete integer values (*i.e.*, ages are not estimated for fractions of years), so age estimates were scaled similar to maturity stages, where the number of individuals in each age class ($nA_i$) replaced the number of individuals in each maturity stage ($nM_m$) and the number of individuals in each age class at each length interval ($n(A_i, FL_l)$) replaced the number of individuals at each maturity stage and FL ($n(M_m, FL_l)$) in equations (1) and (2). There were 16 age classes, 0 to 15 years, which fully encompassed the Atlantic herring ages. The mean length scaled proportion for each age class was computed for all trawls in an analysis area and time interval.

The influence of increased sampling at longer length increments on mean weight was examined by comparing annual mean weights using all the subsample data (*i.e.*, not scaled) and the length-frequency-scaled weight (*i.e.*, scaled). In addition, the mean weight-at-length ($\overline{W(FL)}$) was generated for each trawl haul by calculating the mean weight of all individuals within each sub-sampled length interval (*i.e.*, not scaled by length distribution):

$$\overline{W(FL)} = \frac{1}{n(FL)} \sum_{j=1}^{n(FL)} W_j(FL), \qquad (4)$$

where $Wj$ is individual weight at each fork length interval, and $n(FL)$ is the number of individuals at each sub-sampled length interval. For mean weight-at-length, it is not necessary to scale by the length distribution as the weight-at-length is standardized by taking the mean. In order to calculate a mean weight for the trawl catch from the subsampled data, the scaled mean weight of an individual herring for each trawl haul was calculated by scaling the mean weight-at-length by the length distribution (similar to scaling of maturity and age samples). These scaled mean weights were compared to length-weight relationships derived from the data and those used by the NEFSC (Wigley *et al.*, 2003).

We calculated an index of spawning timing at weekly intervals as the ratio of the combined proportion of prespawning and spawning condition herring (D, R, U maturity codes) relative to the proportion of herring in non-spawning (*i.e.*, postspawned) condition (S and T maturity codes). As the spawning season progresses, the proportion of herring in non-spawning condition should increase so that an indication of peak spawning may be when the ratio of prespawning and spawning-condition herring to postspawned herring transitions from greater than to less than 1.

## Results

There was ample spatial overlap between midwater and bottom trawl hauls in the Georges Bank area, less so in the Gulf of Maine, and very little overlap in southern New

England (Fig. 1). The majority of midwater trawl hauls were clustered in the Georges Bank area, with clusters of sampling in the Jeffreys Ledge (approximately 43° N 70° W) and the mid- to western portion of the Gulf of Maine. Only eleven midwater trawl hauls were conducted in southern New England from 1998 to 2012. In contrast, the bottom trawl hauls were fairly homogeneously distributed throughout the continental shelf north of the mid-Atlantic region. The clusters of bottom trawl hauls in the Great South Channel (approximately 41.5° N 69° W) and Cape Cod Bay (approximately 42° N 72.5° W) were due to comparison tows between the *AL IV* and *HB* that were limited in space and time.

During 1998–2012 the stratified-random survey subsampled 333 to 1004 Atlantic herring per year for a total of 10 679 individual subsamples, while the systematic herring survey subsampled 234 to 7894 Atlantic herring per year for a total of 23 634 individual subsamples. The larger number of individual subsamples from the systematic herring survey is due in part to the way FSCS labels these records. When an individual fish is weighed, it is recorded as a biological subsample, even though it did not have the full biological workup. Thus the systematic herring survey subsample database has numerous fish lengths and weights per centimeter length interval.

Annual mean lengths were similar among midwater and bottom trawl catches in the Georges Bank and Gulf of Maine areas with mean fork lengths ranging from 20 to 26 cm (with the exception of the 11.4 cm mean in 2009 in the Gulf of Maine) and differences in mean lengths of 1 cm or less in 11 of the years between 1998 and 2012 (Fig. 2). Annual mean length was longer from bottom trawl catches in all years and areas except during 2004, 2006, and 2007 in the Gulf of Maine. Differences in annual mean length between midwater and bottom trawl catches were typically less than 1 cm, and were not statistically different (Student's *t*-test, $p<0.05$) in years except 2002, 2005, 2006, 2008, 2010, and 2011 in the Georges Bank area and 2004, 2009, and 2010 in the Gulf of Maine. Temporally, annual mean lengths from both midwater and bottom trawl catches showed a 4–6 year pattern with longest lengths in 2002 and 2006 and shortest lengths in 2004 and 2010 in the Georges Bank and Gulf of Maine areas (Fig. 2). Midwater trawl hauls were conducted in the southern New England area only in 2005 and 2009, rendering inter-annual comparisons between the two surveys impractical. Annual mean lengths from bottom trawl catches were more variable in southern New England than in the other two areas with mean lengths varying by approximately 10 cm (Fig. 2).

A total of 75 trawl hauls, 39 PMRT and 36 4SBT, were conducted as part of the gear comparison (more midwater trawl hauls were completed, but were not used for this analysis) during the Atlantic herring acoustic/midwater trawl survey in 2012. Analyses of mean lengths showed similar results to those from the entire surveys, with statistically longer herring (ANOVA, $p<0.01$) caught in the 4SBT than in the PMRT (Table 1). Mean lengths were not statistically different between day and night for either gear type.

Table 1. Mean lengths (standard deviation in parentheses) and ANOVA results for comparisons of mean length using day and night and gear type (polytron midwater rope trawl (PMRT) and four-seam bottom trawl (4SBT)) as factors. There were a total of 75 trawl hauls, with 39 PMRT and 36 4SBT. The * denotes statistical significance at the 0.01 level.

| | **Mean Length (cm)** | | | | |
|---|---|---|---|---|---|
| | **Gear Code** | | | | |
| **Day/Night** | 4SBT | PMRT | | | |
| Day | 22.5 (0.98) | 22.0 (1.09) | | | |
| Night | 22.3 (1.49) | 21.4 (2.00) | | | |
| | | | **ANOVA** | | |
| | DF | Sum Sq | Mean Sq | *F* value | *P*(>*F*) |
| **Day/Night** | 1 | 3.57 | 3.57 | 1.819 | 0.1819 |
| 4SBT/PMRT | 1 | 8.31 | 8.31 | 4.232 | 0.0435* |
| Day/Night: 4SBT/PMRT | 1 | 0.84 | 0.84 | 0.427 | 0.5158 |
| Residuals | 68 | 133.5 | 1.96 | | |

Mean lengths were calculated at weekly intervals within the Georges Bank and Gulf of Maine areas to explore any intra-seasonal temporal patterns and to compare length distributions between midwater-trawl and bottom-trawl catches. There was at least one week of sampling overlap in the Georges Bank region for all years except 2003, 2009, 2010, and 2012; while in the Gulf of Maine, sampling overlapped only during 2006, 2007, and 2012 (Table 2). During 16 of the 20 weeks where the Georges Bank area was sampled by both surveys, weekly mean lengths were not statistically different (Student's *t*-test, $p<0.05$), but were statistically different (Student's *t*-test, $p>0.05$) during 2 of the 4 overlapping weeks in the Gulf of Maine.

The cumulative length distributions from the midwater and bottom trawl catches in the Georges Bank (Fig. 4) and Gulf of Maine (Fig. 5) areas were bimodal. The smaller mode, both in length and magnitude, was consistently present between 9 and 15 cm and was much less pronounced in the Georges Bank region than in the Gulf of Maine. The large mode was consistently present between 16 and 30 cm and characterized the majority of the herring length distribution. The large mode appears to have smaller modes interleaved. In the Georges Bank area, the length distribution from midwater trawl catches had modes at 18–19, 22, and 24 cm, whereas the length distribution from bottom trawl catches had modes at 22 cm and possibly at 18 and 27 cm, and was slightly skewed towards longer lengths (Fig. 4). In the Gulf of Maine, the length distribution from midwater trawl catches had a mode at 12 cm and a multimodal distribution between 17 and 30 cm with modes at 18, 21, 24, and possibly 28 cm; whereas the length frequency distribution from bottom

Table 2. Atlantic herring mean length ($\bar{L}$), standard error (**SE**), and t-statistic from midwater trawl (**MWT**) and bottom trawl (**BT**) catches during the same week (**Week**) in the Georges Bank (**GB**) and Gulf of Maine (**GoM**) analysis areas. NA denotes a single trawl, so no statistical inference was generated. Asterisks denote significance at the 5% level.

| Area | Year | Week | MWT $\bar{L}$ (cm) (SE) | BT $\bar{L}$ (cm) SE | *t*-statistic |
|---|---|---|---|---|---|
| GB | 1998 | Oct. 8–15 | 23.9 (0.33) | 23.3 (0.59) | 0.417 |
| GB | 1999 | Oct. 8–15 | 24.5 (0.18) | 24.6 (0.36) | -0.322 |
| GB | 2000 | Sept. 22–30 | 25.0 (0.25) | 24.9 (0.79) | 0.026 |
| GB | 2000 | Oct. 1–7 | 25.1 (0.16) | 26.2 (0.42) | -1.034 |
| GB | 2001 | Sept. 22–30 | 24.2 (0.25) | 20.4 (2.11) | 1.441 |
| GB | 2001 | Oct. 1–7 | 23.5 (0.14) | 25.2 (0.42) | -1.575* |
| GB | 2001 | Oct. 8–15 | 22.5 (0.44) | 25.2 (0.88) | -1.773* |
| GB | 2002 | Oct. 1–7 | 24.7 (0.21) | 25.8 (0.70) | -0.874 |
| GB | 2002 | Oct. 8–15 | 24.9 (NA) | 25.8 (0.23) | NA |
| GB | 2004 | Oct. 8–15 | 22.9 (1.23) | 22.9 (0.80) | 0.007 |
| GB | 2005 | Oct. 8–15 | 23.7 (0.43) | 25.6 (0.73) | -1.717 |
| GB | 2006 | Sept. 22–30 | 24.0 (0.27) | 23.8 (0.17) | 0.285 |
| GB | 2006 | Oct. 1–7 | 24.3 (0.21) | 25.6 (0.35) | -1.593* |
| GB | 2006 | Oct. 8–15 | 24.4 (0.28) | 26.4 (0.40) | -1.882* |
| GoM | 2006 | Oct. 1–7 | 24.3 (0.12) | 26.5 (NA) | NA |
| GB | 2007 | Oct. 8–15 | 25.2 (1.10) | 25.0 (0.16) | 0.207 |
| GB | 2007 | Oct. 16–23 | 24.3 (0.45) | 24.8 (0.28) | -0.433 |
| GB | 2007 | Oct. 24–31 | 24.6 (0.29) | 25.0 (0.42) | -0.700 |
| GoM | 2007 | Oct. 8–15 | 25.2 (NA) | 26.8 (0.44) | NA |
| GoM | 2007 | Oct. 16–23 | 24.8 (1.24) | 23.3 (0.53) | 1.97* |
| GB | 2008 | Oct. 1–7 | 23.8 (1.11) | 23.9 (NA) | NA |
| GB | 2008 | Oct. 8–15 | 24.3 (0.33) | 25.2 (0.29) | -0.792 |
| GB | 2011 | Oct. 8–15 | 22.2 (0.39) | 20.9 (NA) | NA |
| GoM | 2012 | Oct. 16–23 | 22.3 (0.30) | 21.9 (0.63) | 0.80* |

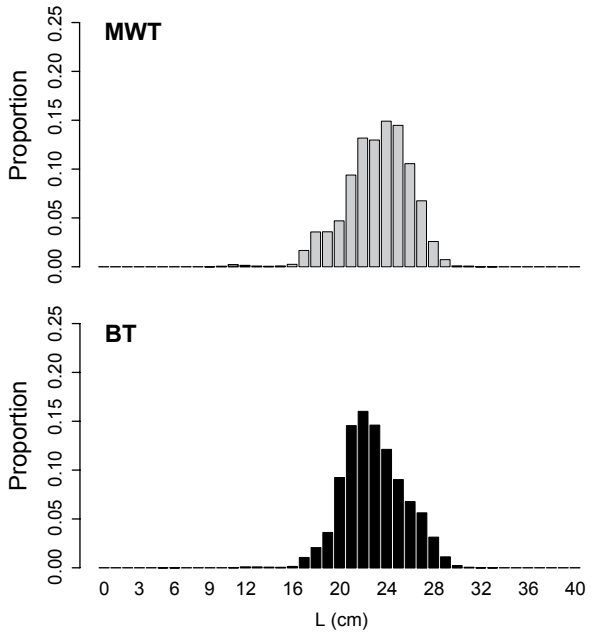


Fig. 4. Cumulative length-frequency distributions for midwater trawl (**MWT**) (top panel) and bottom trawl (**BT**) (bottom panel) catches over all years (1998–2012) within the Georges Bank analysis area.

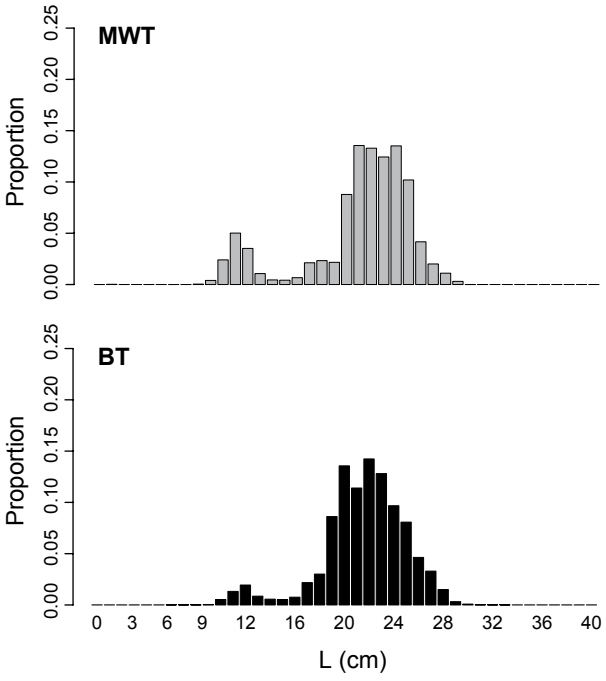


Fig. 5. Cumulative length-frequency distributions for midwater trawl (**MWT**) (top panel) and bottom trawl (**BT**) (bottom panel) catches over all years (1998–2012) within the Gulf of Maine analysis area.

trawl catches had modes at 13 cm and a multimodal distribution between 17 and 30 cm, with modes at 20 and 22 and possibly at 17 and 27 cm (Fig. 5).

The influence of increased sampling at longer length increments on mean weight was examined by comparing annual mean weights using all the subsample data (*i.e.*, not scaled) and the length-frequency-scaled weight (*i.e.*, scaled). Annual mean weights were typically heavier for unscaled weight than for scaled weight (Fig. 6) and this trend was independent of gear type. Mean scaled weight was typically 3 to 20 g lighter for both gear types in the Georges Bank and Gulf of Maine areas, but were not statistically different (Student's *t*-test, $p<0.05$) except for midwater trawl catches during 2002, 2005, 2006, and 2008 in the Georges Bank region and in 2000 and 2003 the Gulf of Maine, and for bottom trawl catches in the Georges Bank region during 2011. There were years (*e.g.*, 2011 and 2012) in the Georges Bank and Gulf of Maine where the scaled weight values were similar to or actually heavier than the unscaled mean weights; although the differences were small, typically less than 1 g. These years reflected periods when there were fewer large herring subsampled, as evidenced by the lower mean weights and greater proportion of younger fish (see below), and thus less oversampling at longer length intervals.

The scaled annual mean weights for the Georges Bank and Gulf of Maine regions ranged from 62 to 159 g for both midwater and bottom trawl catches during 1998 to 2012, with the exception of 14 g in 2009 which was the lowest value recorded (Fig. 7). Mean scaled weights between midwater and bottom trawl catches were typically within 10 g of each other and were not statistically different (Student's *t*-test, $p<0.05$) except in the Gulf of Maine in 2003, 2004, and 2009. Mean scaled weights were more variable in the southern New England region in comparison to the northern areas, with mean weight varying by almost 100 g. Temporally, mean weight showed a nearly identical pattern to mean length (Fig. 2) with a 4–6 year pattern with heaviest weights in 2000 and 2006 (Fig. 7).

In nearly all years and length classes, mean weight-at-length was greater in midwater trawl catches than in bottom trawl catches (Georges Bank data in 2005 is shown in Fig. 8). Mean weight-at-length increased nearly logarithmically, and in most years did not plateau at maximum lengths (Fig. 8). The length-weight relationship ($\ln(W)=\ln(a)+b*\ln(L)$) (Wigley *et al.*, 2003) for Atlantic herring derived from the full set of subsamples consistently predicted individual weight within a few percent of the mean weight-at-length for both bottom and midwater trawl.

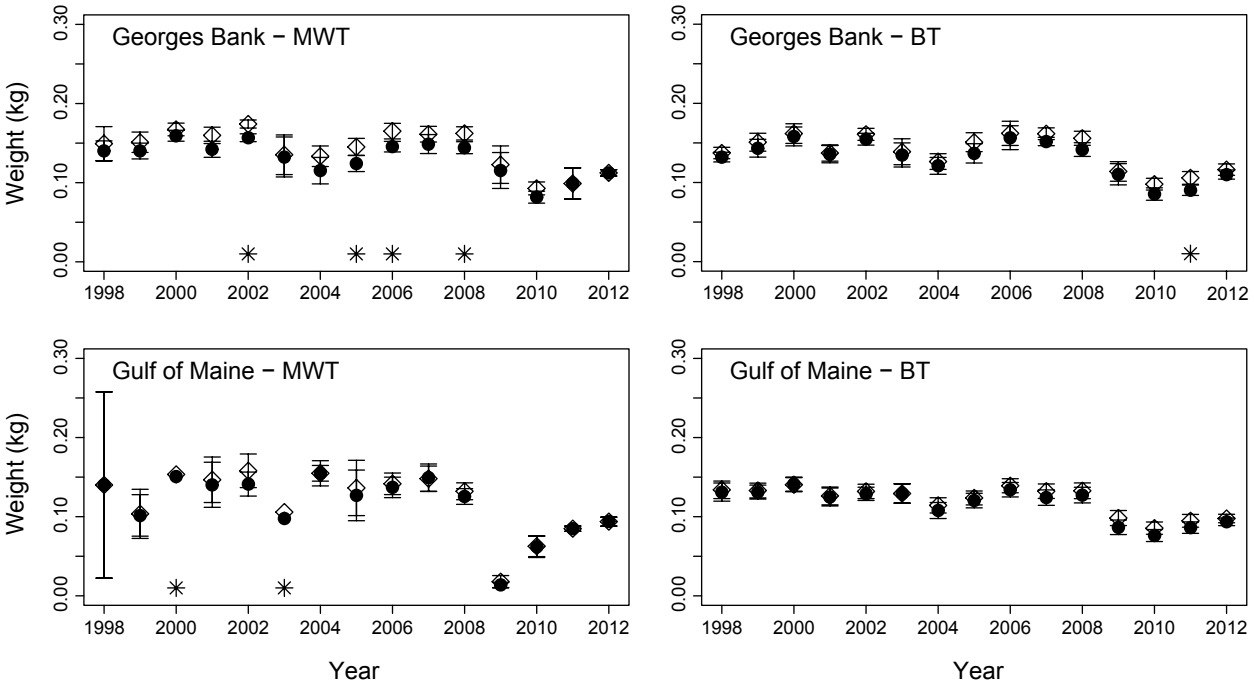


Fig. 6. Annual mean weight without correcting for length distribution (open diamonds) from midwater trawl (**MWT**) and bottom trawl (**BT**) catches in the Georges Bank and Gulf of Maine analysis areas. Annual mean weights (solid circles) scaled by the length distribution from MWT and BT catches in the Georges Bank and Gulf of Maine analysis areas. Asterisks indicate significant differences between length scaled and uncorrected mean weights at the 5% level.

Atlantic herring age classes scaled by length distribution showed similar trends and patterns between midwater and bottom trawl catches in the Georges Bank and Gulf of Maine regions, and there did not appear to be any consistent differences in trends of age classes between the two trawl types (Fig. 9). While age class trends were similar, it appears that younger fish tended to be sampled better by midwater trawl hauls and older fish tended to be sampled better by bottom trawl hauls. Two large year classes were detected at age two in 2003 and age one in 2009 by midwater trawl catches in the Gulf of Maine, but these age class were not well sampled by bottom trawl catches. There appears to be a slightly greater proportion of age six and older herring in the Gulf of Maine than in the Georges Bank region, with only one year (2008) where age six herring were caught in southern New England. Younger aged herring were caught in southern New England when compared to Georges Bank and Gulf of Maine in 2003, 2011, and 2012. There appears to be a 3–4 year cycle of cohorts in the Georges Bank and Gulf of Maine regions, but no temporal pattern is discernible in southern New England.

In the Georges Bank region, midwater trawl catches had greater proportions of Atlantic herring in prespawning condition and bottom trawl catches had greater proportions of adult herring in non-spawning condition in all years except 2007; and bottom trawl catches had greater proportions of herring in spawning condition in nine of the 15 years (Fig. 10). Those trends were similar in the Gulf of Maine with greater proportions of prespawning herring caught in midwater trawls and greater proportions of adult herring in non-spawning condition caught in bottom trawls. In the Gulf of Maine, midwater trawl catches showed greater proportions of prespawning herring prior to 2006, whereas there were greater proportions of adult herring in non-spawning condition after 2006. Both midwater and bottom trawl catches in the Georges Bank region and bottom trawl catches in the Gulf of Maine showed peaks in the proportion of immature herring in 2004 and 2010. In the Gulf of Maine, proportion of immature herring in midwater catches peaked in 1999, 2003, and 2009, which except for 1999 were one year prior to peaks in the Georges Bank region; but peaks of immature herring in bottom trawl catches in the Gulf of Maine coincided with those in the Georges Bank area. Bottom trawl catches in southern New England had high proportions of immature and spawning condition herring and low proportions of adult non-spawning herring throughout the years.

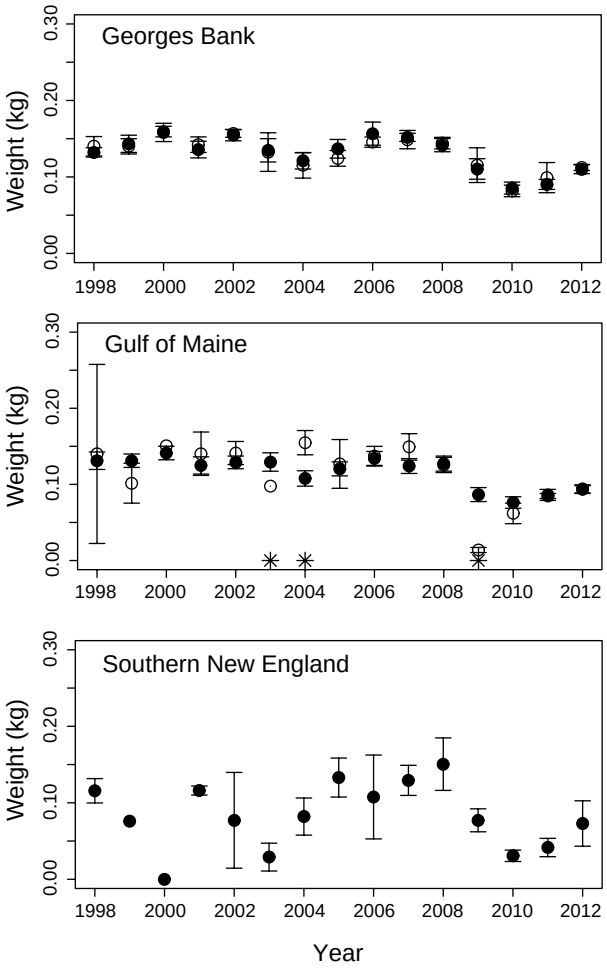


Fig. 7. Annual Atlantic herring mean weight in the Georges Bank (top panel), Gulf of Maine (middle panel), and southern New England (bottom panel) analysis areas for midwater trawl (open circles) and bottom trawl (solid circles) catches. Error bars are 95% confidence interval. Points with no error bars denote years where only one trawl occurred in that area. Asterisks indicate significant differences between mean weights at the 5% level.

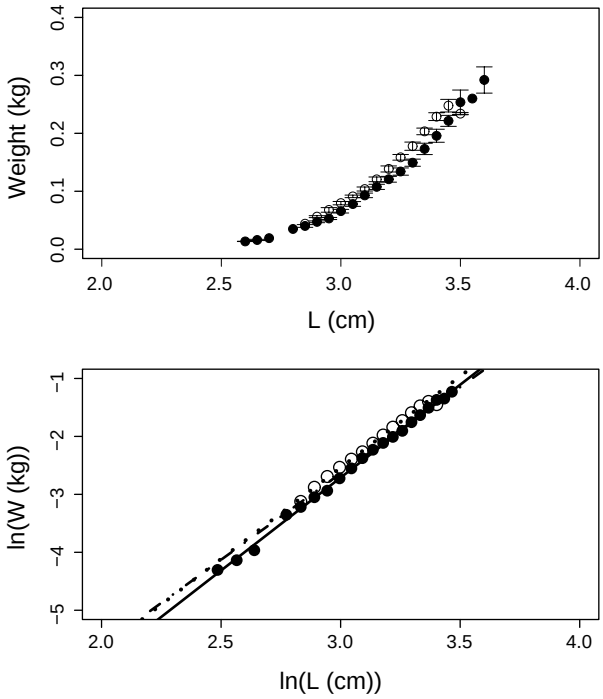


Fig. 8. Mean weight at each 1-cm length interval for Atlantic herring in the Georges Bank (top panel) analysis area for midwater trawl (open circles) and bottom trawl (solid circles) catches in 2005. Error bars are 95% confidence interval. Points with no error bars denote years where only one trawl occurred in that region. Length weight relationships (bottom panel) for midwater trawl (open circles) and bottom trawl (solid circles) catches and logarithmic regressions for midwater trawl (dashed line), bottom trawl (solid line), and historical length weight regressions (Wigley *et al.*, 2003) (dot-dash line).

The index of spawning timing suggested peak spawning occurred from September into early October (Fig. 11). In the Georges Bank region, the transition from prespawning and spawning condition herring to postspawned herring tended to be during the second and third week of October, with some transitions occurring in September. In general, once the transition occurred, the proportion of postspawned herring dominated, but in some years (*e.g.*, 2005), the transition occurred multiple times during the spawning season. In the Gulf of Maine, the transition tended to be earlier than in the Georges Bank region, with transitions occurring in late September and early October (Fig. 11).

## Discussion

The overall similarity of biological metrics between midwater and bottom trawl catches suggests both gear types provide comparable samples of the core demographics (length, weight, age, maturity) of Atlantic herring in the Georges Bank and Gulf of Maine regions in autumn. Our results indicate that each data set can be used separately or combined, for example in cases where neither survey provides sufficient spatial or temporal coverage. Within analysis areas, annual mean lengths and weights and temporal patterns of herring size were consistently similar between gear types. Historically, there was concern that a bottom trawl may not adequately sample a pelagic species such as Atlantic herring (TRAC, 2012) (Overholtz *et al.*, 2006) and in the absence of quantitative information, catchability among gear types have been set to 1 (Anonymous, 2012) or allowed to be a

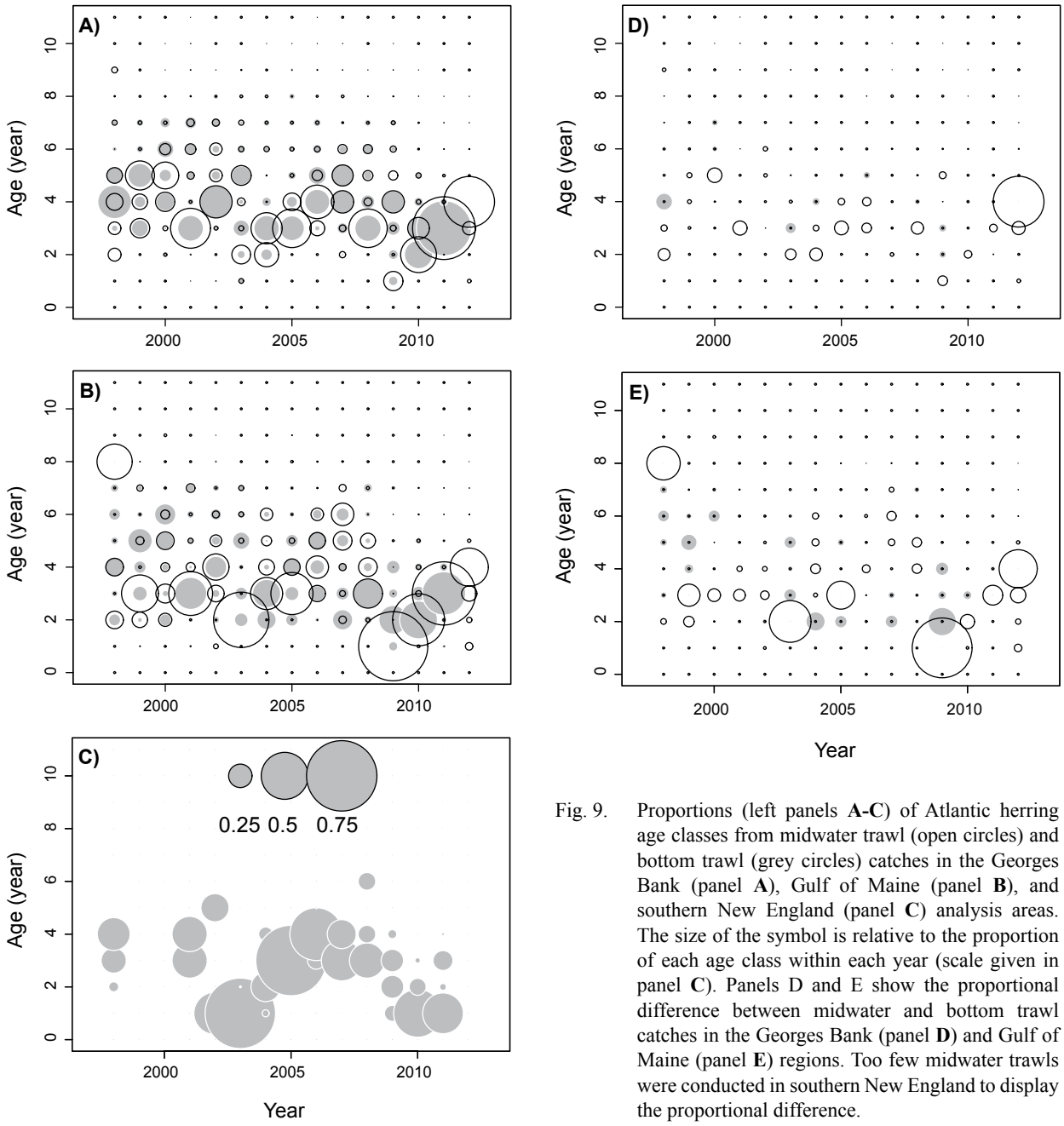


Fig. 9. Proportions (left panels **A-C**) of Atlantic herring age classes from midwater trawl (open circles) and bottom trawl (grey circles) catches in the Georges Bank (panel **A**), Gulf of Maine (panel **B**), and southern New England (panel **C**) analysis areas. The size of the symbol is relative to the proportion of each age class within each year (scale given in panel **C**). Panels D and E show the proportional difference between midwater and bottom trawl catches in the Georges Bank (panel **D**) and Gulf of Maine (panel **E**) regions. Too few midwater trawls were conducted in southern New England to display the proportional difference.

free parameter in assessment models (NEFSC, 2012). This study does not investigate catchability per se, but is the first comparison of demographic information from fisheries-independent bottom and midwater trawl sampling of Atlantic herring in the Georges Bank and Gulf of Maine regions, and to our knowledge the first comparisons of bottom and midwater trawl catches of Atlantic herring. Whether these similarities can be extended to other areas and time periods (*e.g.*, overwintering in the mid-Atlantic) remains to be investigated. There is evidence that bottom and midwater trawls can provide comparable biological data (*e.g.*, Pillar and Barange, 1995). In a series of papers, Stockwell *et al.* (2006; 2007) and Yule *et al.* (2007; 2009) showed substantial differences in abundance and biomass estimates of a semi-pelagic species in Lake Superior between bottom trawl and acoustic/midwater trawl surveys, yet length distributions were consistently similar between gear types.

Atlantic herring in the northeastern U.S. are fall spawners and aggregate near spawning grounds for days, potentially weeks, prior to spawning while their

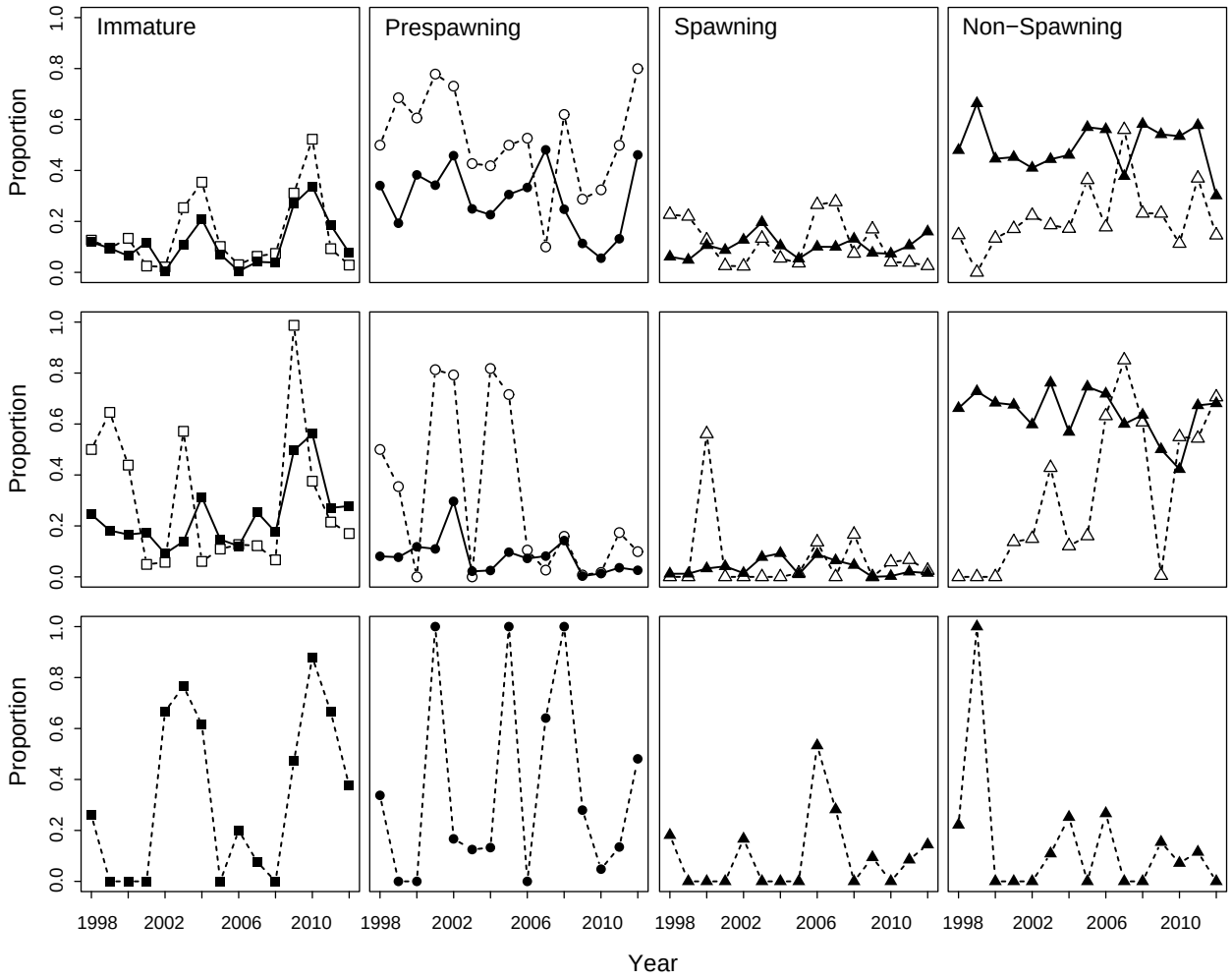


Fig. 10. Proportion of immature, prespawning, spawning condition (ripe, ripe and running maturity stages), and non-spawning condition (spent and resting) Atlantic herring in the Georges Bank (top row), Gulf of Maine (middle row), and southern New England (bottom row) analysis areas. Open symbols denote midwater trawl catches and solid symbols denote bottom trawl catches.

gonads develop. These prespawning aggregations in the Georges Bank region can extend for miles (Jech and Michaels, 2006; Makris *et al.*, 2009), but only a portion of the aggregation spawns at any one time (*e.g.*, Skaret *et al.*, 2003; Stephensen *et al.*, 2009). To explore timing of spawning, we looked at the transition from prespawning and spawning to postspawning maturity as an index for peak spawning. Neither survey consistently covered the transition period, so combining the surveys into seasonal time series was necessary to evaluate spawning timing. If the earliest occurrence of the transition period can be used as a proxy for peak spawning, this index suggests peak spawning generally occurs earlier in the Gulf of Maine than in the Georges Bank region, and there is asynchrony in spawning between the Gulf of Maine herring and Georges Bank herring. In the Georges Bank region, the earliest occurrence of the transition period occurred during the second or third week of October in 10 of 15 years, and in the Gulf of Maine, the transition occurred prior to the second week of October in 7 of 15 years, suggesting earlier spawning in the Gulf of Maine. This is consistent with historical spawning behavior where herring spawn earlier in further north spawning grounds (*e.g.*, Stephenson *et al.*, 2009). There appears to be asynchrony in the earliest spawning periods between the Gulf of Maine and Georges Bank. The earliest transition periods occurred during the third week of September in 2004 and 2005 in the Georges Bank regions, whereas there were two cycles, 2002–2003 and 2008, in the Gulf of Maine (gray line in Fig. 11). However, the uneven sampling early in the season in the Gulf of Maine potentially influences this supposition (*e.g.*, lack of sampling in Sept. in 2009 and 2010), so additional data such as fisheries-dependent data will be required to

evaluate whether there is a connection between herring spawning on Georges Bank and in the Gulf of Maine. The underlying process of spawning timing are not completely understood, but are most likely related to environmental and biological factors and spawning timing can be quite adaptable to changing pelagic and benthic habitat (Geffen, 2009; Melvin *et al.*, 2009). Further investigations as to habitat changes in relation to spawning timing and differences between Gulf of Maine and Georges Bank habitat may explain these observations.

Although spawning timing may not be linked, similarity in age structures between Georges Bank and the Gulf of Maine coupled with similarities in abundance trends (Jech and Sullivan, 2014) suggest a connection (*i.e.*, a common response to intrinsic and/or extrinsic factors) between Gulf of Maine herring and Georges Bank herring. There are four to five year classes between 1998 and 2012 that coincide in both the Gulf of Maine and Georges Bank. The two strong year classes, one beginning in 2003 and the other in 2009, dominate the herring assessment for the past decade and it is thought the 2009 year class is one of the strongest on record (Anonymous, 2012). The other cohorts in 2000, 2006, and one that predates 1998 are not as strong, but are similarly represented in both regions. Atlantic herring are assessed as one large population that is subdivided by geography (Overholtz, 2002), but multiple "subpopulations" or "stocks" (*e.g.*, Georges Bank, coastal Maine, Bay of Fundy) are thought to comprise this larger population (McQuinn, 1997; Cadrin *et al.*, 2004; Stephensen *et al.*, 2009). Unfortunately, similarities in age structure and abundance alone do not confirm or refute connectedness among Georges Bank and Gulf of Maine herring. Other supporting information such as morphometrics (*e.g.*, Cadrin *et al.*, 2004), genetics (*e.g.*, McQuinn, 1997), movement and migration (*e.g.*, Kanwit and Libby, 2009), and philopatry or at least some level of spawning in natal locations (*e.g.*, Stephensen *et al.*, 2009) are needed to confirm population structure.

Combining the data sets revealed interesting features of population structure, but treating data from each gear type independently also exposed some noteworthy patterns. Juvenile herring tended to be caught in higher proportion by midwater trawls than bottom trawls, suggesting juvenile herring occupy the water column more so than demersal or benthic areas in the Gulf of Maine, which is consistent with accounts of juvenile herring predominately occurring in the water column and/or near shore (*e.g.*, Hallfredsson and Pedersen, 2009). On the opposite end of the length, weight, and age spectrum, longer, lighter, and older fish tended to be caught in higher proportions by the bottom trawl. Adult prespawning Atlantic herring in the Georges Bank region tend to occupy the 150–200 m depth

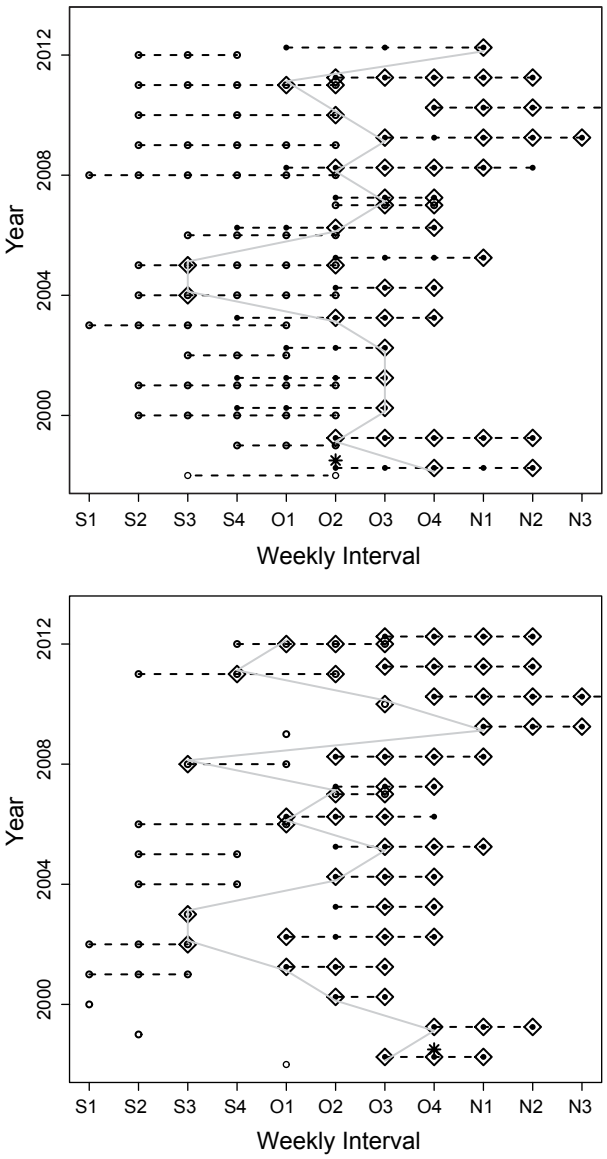


Fig. 11. Weekly maturity indices in the Georges Bank (top panel) and Gulf of Maine (bottom panel) areas. Weekly intervals are given as the week (1 is the first week of the month, 2 is the second week, etc.) of the month (S is September, O is October, and N is November). Each line corresponds to maturity indices for midwater trawl (open circles) and bottom trawl (solid circles) catches for each week for each year. The bottom trawl symbols are offset from the midwater trawl symbols to prevent symbol overlap. The open diamonds represent weeks where the proportion of adult non-spawning condition herring was greater than the proportion of prespawning and spawning condition herring (*i.e.*, more herring had spawned or were resting than were preparing to spawn or spawning). The grey line connects the earliest occurrence of the transition from prespawning and spawning to postspawned condition among years.

zone (Nero *et al.*, 2004; Gong *et al.*, 2009) while queuing to spawn. Stanton *et al.* (2012) showed that length ranges of adults were fairly narrow within these prespawning aggregations, so the largest and oldest of the adults may be more oriented to the seabed than the younger adults. The reasons for this apparent preference are unknown. It may be due to physiological reasons, where, for example, swimbladders of the older herring may lose gas at a faster rate than younger herring and are not able to keep the swimbladder inflated as well while they develop gonads. Alternatively, Atlantic herring spawn on gravel and cobble substrate, and it may be that the older herring act as the guides to the spawning grounds. Both of these are speculative and it would be interesting to know whether the differences we measure are indicative of biological or behavioral patterns.

The age structure was narrower in the Georges Bank region (predominately ages 3–5) than in the Gulf of Maine where a greater proportion of immature (age 1 and 2) herring were captured in midwater trawls and a greater proportion of older herring were captured in bottom trawls. Juvenile herring tend to shallower water and/or more inshore areas than do adults (Creaser *et al.*, 1984; Creaser and Libby, 1988), so Georges Bank juveniles may not reappear on Georges Bank until they mature. At the opposite end of the age spectrum, there appears to be fewer age 6 + herring in the Georges Bank region and why this is or should be so is not readily apparent from these data. However, information on younger age classes may be more important to understanding stock structure than understanding adult behavior (TRAC, 2012). The two strong year classes in 2003 and 2009 are highlighted in the proportion of immature herring caught in midwater and bottom trawls in the Georges Bank and Gulf of Maine regions. In the Georges Bank area, years of peak proportions of immature herring matched between midwater and bottom trawl catches, but in the Gulf of Maine years of peak proportions of immature herring caught in bottom trawl catches lagged by one year those from midwater trawl catches. These peaks were dominated by age 2 herring. Interestingly, what appears to be a strong year class in 1999 based on midwater trawl samples in the Gulf of Maine does not proliferate as strongly as the other two year classes. One apparent difference between this 1999 peak and the other two at 2003 and 2009 is that the peak was not reflected in Gulf of Maine bottom trawl catches.

Sampling of historical spawning sites appears to characterize the biological state of Atlantic herring in the Gulf of Maine. The systematic herring survey annually surveyed historical spawning sites (Overholtz *et al.*, 2006) in the Georges Bank and Gulf of Maine areas, whereas the stratified-random survey covered the entire area. In terms of biological metrics, results presented here suggest that Atlantic herring do not need to be intensively sampled throughout the entire region – at least for the Georges Bank stock - but sampling at selected sites may provide sufficient demographic information that is representative of the individual stocks and potentially the overall population. Implementing a subsampling scheme that takes into account spatial factors may result in an efficient sampling design with comparable precision to historical data.

## Conclusions

Broad similarities in Atlantic herring biological metrics between midwater and bottom trawl catches suggest both gear types provide comparable sampling of herring demographics in the Gulf of Maine and Georges Bank regions during autumn and data from each gear type can be used separately or combined to make a complementary data set. Within regions, annual mean lengths and weights and temporal patterns of herring size were consistently similar between gear types. Length, weight, and age distributions were similar between gear types and showed similar spatial and temporal patterns. Similarity in age structures between Georges Bank and the Gulf of Maine coupled with similarities in abundance trends suggest a connection (*i.e.*, a common response to intrinsic and/or extrinsic factors) between inshore and Gulf of Maine herring and Georges Bank herring, but potential asynchrony in spawning timing suggests independence between these herring stocks. Overall similarities can mask interesting patterns, such as midwater trawls appeared to sample younger fish and bottom trawls appeared to sample older fish, and midwater trawls sampled smaller but heavier herring than did bottom trawls. Sampling of historical spawning sites appears to characterize the biological state of Atlantic herring in the Georges Bank region and could be utilized to design an efficient sampling scheme for Atlantic herring in the Gulf of Maine.

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# The biology of *Benthosema glaciale* and *Ceratoscopelus maderensis* (Myctophidae) in the Slope Sea off Nova Scotia, Canada

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## Abstract

The myctophid species *Benthosema glaciale* and *Ceratoscopelus maderensis* were predominant in the catches of 10 mesopelagic fish surveys conducted in the Slope Sea, south and southeast of Nova Scotia. The area surveyed included both cold northeastern (Labrador Slope Water – LSW) and warm southwestern (Warm Slope Water – WSW) components of this water mass. The sub-polar-temperate species, *B. glaciale*, was found to be only about 15% as abundant in WSW as in LSW. Nonetheless, it occurred throughout WSW and reproduced there, maturing at a younger age than in LSW. The temperate species, *C. maderensis*, the predominant myctophid caught in WSW, had a life cycle of one yr. in most cases, but a small proportion lived for a second year and these occurred primarily in LSW. These larger animals matured sexually and contributed to spawning in the LSW/WSW boundary area, but their reproductive contribution elsewhere in LSW and in continental slope waters remains to be established. Both species had diverse diets, the taxonomic compositions of which overlapped substantially.

*Keywords*: Myctophid, Scotian Shelf, Slope Sea, *Benthosema glaciale, Ceratoscopelus maderensis*



## Introduction

The Canadian Department of Fisheries and Oceans (DFO) conducted a series of mesopelagic fish surveys in 1984–89 in an area that extended from about 50°W, south of Grand Bank, to about 64°W, off the western Scotian Shelf (Fig. 1). This area is the north-eastern part of an oceanographic water body, named the Slope Sea by Csanady and Hamilton (1988), that extends to Cape Hatteras in the southwest. Its northern edge is the continental slope and its southern edge the Gulf Stream (GS). It is occupied in the southwest by Warm Slope Water (WSW) and in the northeast by cold Labrador Slope Water (LSW), the location of the boundary between these varying substantially depending on the volume of cold water transported around the tail of Grand Bank.

Backus *et al*. (1977), in a review of Atlantic mesopelagic zoogeography, recognized WSW as the most westerly province in a North Atlantic temperate region, the adjacent LSW being the most southwesterly component of a subarctic region to the northeast. Thus, the DFO surveys were designed to include sampling locations in both WSW and LSW.

An inventory of the mesopelagic fishes caught during the DFO surveys (Themelis and Halliday, 2012) identified the myctophids *Benthosema glaciale* (Reinhardt, 1837) (the glacier lanternfish) and *Ceratoscopelus maderensis* (Lowe, 1839) (the horned lanternfish) as the dominant species in catches in LSW and WSW respectively. The present paper examines and compares the biology of these two species in these water masses, to provide a fuller understanding of their status in each area and thus improve knowledge of the biogeography of the Slope Sea. Biological features examined are distribution, growth, reproduction and diet. Larval distributions over the continental slope are described also based on data from

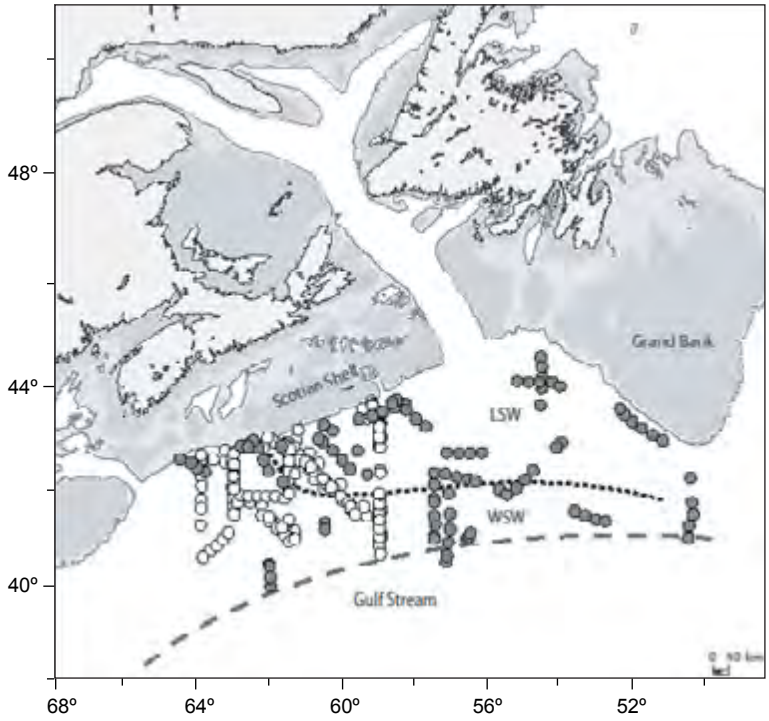


Fig. 1. Location of sampling by midwater trawl in the Slope Sea from 1984 to1989. (Dark circles - exploratory cruises, light circles - standard cruises.) Dashed and dotted lines are indicative of the locations of the boundaries between the Gulf Stream and Warm Slope Water (WSW) and WSW and Labrador Slope Water (LSW) masses, respectively.

ichthyoplankton surveys conducted by DFO (O'Boyle *et al*., 1984) and the USA National Marine Fisheries Service (NMFS) (Morse *et al*., 1987).

## Methods

Ten surveys were conducted in the period 1984–89. The number of tows conducted in each water mass on each survey is listed in Table 1. Listings of station coordinates and maps are available in Halliday *et al*. (1995). The first four surveys were exploratory, and areas fished extended variously from about 50°–65°W and from the shelf edge to 40°N (Fig. 1). The subsequent six standardized cruises were conducted between February 1988 and August 1989, arranged temporally to provide sampling every second calendar month and restricted spatially to 59°–64°W and from the shelf edge to about 41°N. Sampling on these standardized surveys was conducted along three north-south transects at 59°, 61°30' and 64°W linked by diagonal transects. This sampling block was chosen because the exploratory cruises had shown that it typically contained both LSW and WSW.

The sampling gear used was an International Young Gadoid Pelagic Trawl (IYGPT) (Hislop, 1970), a twin-warp mid-water trawl with an 11.5 m (horizontal) by 8.5 m (vertical) mouth opening (measured using a SCANMAR net management system). A three-step oblique night tow, with the net towed for 10 min. at 200, 100 and 50 m, was adopted as a standard deployment. Night was defined as extending from one hour after sunset to one hour before sunrise. Total fishing time including haul back was about 40 min. On the first survey (H127) the third step was at about 20 m and on the second survey (N057) depth monitoring gear failed and continuous oblique tows from 200-300 m to the surface were conducted, but the results from these are accepted as comparable to those from subsequent standard tows.

Other, non-standard, IYGPT tows were made opportunistically during the day and those made at depths of 350–1000 m are used here to describe deep water daytime catches. Only those tows made at locations where bottom depth was greater than 1000 m are used to avoid shelf edge effects on catches.

Profiles of water temperatures from the surface to at least 460 m (and sometimes as deep as 1830 m) were collected at all fishing stations, and at intermediate locations. A description of oceanographic equipment and methodologies used, station distributions, and an analysis of the hydrographic data collected, are provided by Halliday *et al*. (1995).

Previous studies of mid-water fishes in the Northwest Atlantic have defined water masses by temperatures at 200 m as follows: LSW<9°C; 9°C ≥ WSW <15°C; GS≥ 15°C; (after Worthington, 1964), and these criteria were used here to classify fishing stations by water mass in summer surveys. However, in winter, it was found that 'transition areas' between water masses occurred when WSW was overlain by a cold upper layer. Tows in such transition areas were combined with those clearly in WSW in October and December surveys and with those clearly in LSW in February, based on overall faunal similarities (Themelis, MS 1996).

All fishes were separated from catches at sea and preserved in 10% formalin. On subsequent examination ashore, these were identified to species, categorized as larvae (pre-metamorphic) or adults (post-metamorphic) and, within each of these categories, the number caught and their minimum and maximum sizes ((standard length - SL) to the nearest mm)) were recorded. Specimens were then transferred to 50% isopropanol for long-term preservation and archived at the Atlantic Reference Centre, Huntsman Marine Science Centre, St. Andrews, N.B., Canada.

Table 1. Median numbers per standard night tow of *B. glaciale* and *C. maderensis* by water mass in standard and non–standard cruises, and number of tows. (Dashes indicate no sampling.)

| Month | Standard Cruises | | | | Non–standard Cruises | | | |
|---|---|---|---|---|---|---|---|---|
| | Cruise/ Year | GS/ WCR | WSW | LSW | Cruise/ Year | GS/ WCR | WSW | LSW |
| | | | | ***Benthosema glaciale*** (no./tow) | | | | |
| Feb. | N096/1988 | – | 96 | 164 | N057/1986 | 4 | 32 | 24 |
| Apr. | N119/1989 | – | 465 | 1247 | – | – | – | – |
| June | N122/1989 | 0 | 43 | 943 | – | – | – | – |
| Aug. | N126/1989 | – | 30 | 219 | N067/1986 | – | 8 | 62 |
| Sept. | – | – | – | – | N089/1987 | 0 | 0 | 302 |
| Oct. | N110/1988 | – | 3 | 45 | H127/1984 | 0 | 1 | 299 |
| Dec. | N112/1988 | 0 | 23 | 159 | – | – | – | – |
| | | | | ***Ceratoscopelus maderensis*** (no./tow) | | | | |
| Feb. | N096/1988 | – | 328 | 18 | N057/1986 | 12 | 169 | 29 |
| Apr. | N119/1989 | – | 193 | 21 | – | – | – | – |
| June | N122/1989 | 0 | 116 | 68 | – | – | – | – |
| Aug. | N126/1989 | – | 185 | 41 | N067/1986 | – | 127 | 33 |
| Sept. | – | – | – | – | N089/1987 | 0 | 143 | 24 |
| Oct. | N110/1988 | – | 172 | 25 | H127/1984 | 64 | 1368 | 39 |
| Dec. | N112/1988 | 53 | 322 | 19 | – | – | – | – |
| | | | | ***Number of Tows*** | | | | |
| Feb. | N096/1988 | – | 5 | 13 | N057/1986 | 1 | 5 | 7 |
| Apr. | N119/1989 | – | 5 | 4 | – | – | – | – |
| June | N122/1989 | 3 | 5 | 5 | – | – | – | – |
| Aug. | N126/1989 | – | 9 | 9 | N067/1986 | – | 17 | 10 |
| Sept. | – | – | – | – | N089/1987 | 4 | 12 | 8 |
| Oct. | N110/1988 | – | 20 | 14 | H127/1984 | 2 | 5 | 3 |
| Dec. | N112/1988 | 5 | 19 | 10 | – | – | – | – |

The metric chosen to describe relative abundance (density) was the median of catch numbers per tow, as numbers per tow were not normally distributed and zero catches occurred regularly, making both arithmetic and geometric means unsuitable.

Subsets of the catches of *B. glaciale* and *C. maderensis* from each of the six standard cruises in 1998–99 were arbitrarily selected from each water mass for examination in detail. From each selected sample, up to 300 fish were measured for standard length (larger catches being randomly sub-sampled). From these, length-stratified subsamples were examined for sex, maturity, fecundity and stomach contents.

The sexual development of females of both species was classified into the stages immature, ripening (occurrence of visible eggs), ripe (occurrence of some hydrated eggs), spent (occurrence of residual eggs), or resting. Maturity ogives were calculated as the ratio of numbers at ripening, ripe and spent stages to the total at all stages, by length group, during the defined spawning season. The 'total at all stages' category included half of those specimens too small for sex to be determined (typically fish <25 mm). In contrast to females, the reproductive organs of males did not exhibit features that provided an objective basis for estimating size at maturation. In *B. glaciale*, however, the state of development of luminous caudal glands (a single supracaudal gland on males and a pair of smaller infracaudal glands on females) was noted, as the occurrence of these has been associated with sexual maturation (Gjøsæter, 1981; Kawaguchi and Mauchline, 1982).

Fecundity estimates were obtained by counting all maturing eggs in the ovaries of those female individuals classed as "ripe", *i.e.* those in which some hydrated eggs were observed.

Stomach fullness was assessed visually as empty (coded 0), containing a small amount of food (1), about ½ full (2), full (3) or distended (4), following Gjøsæter (1973). The proportion of the contents (by volume) that could not be assigned to a taxonomic group because of digestion was classified as nil (0), less than ¼ (1), ¼ to ½ (2), ½ to ¾ (3), ¾ to <1 (4) and all (5).

Information on larval distributions was extracted from the data archives for the ichthyoplankton surveys conducted over the Scotian Shelf by DFO in 1976–82 (O'Boyle, *et al*., 1984) and over shelf waters adjacent to the USA coast by NMFS in 1977–87 (Morse *et al*., 1987). Both survey series extended seaward into continental slope waters and sampling was distributed over all months of the year. Catch numbers of *B. glaciale* and *C. maderensis* were summed by month and by longitude to provide an account of temporal and spatial distribution of catches. No corrections were made to account for differences in fishing effort among months or areas.

## Results

### *Benthosema glaciale*

#### Distribution

The median catch per tow of *B. glaciale* in IYGPT standard night tows (Table 1) was higher in LSW than it was in WSW in all but the first exploratory survey. Among the six standard surveys, the lowest differentials between water masses were observed in samples from February and April (ratio of LSW/WSW = ~x2 and ~x3 respectively) whereas for the other four surveys this ratio was in the range x7–x22. The median of the ratios for all six standard surveys was x7. However, in the deep day tows conducted during standard surveys, the differential in density between LSW and WSW was about x3 in both winter (December–April) and summer (June–October) (Table 2).

#### Length compositions by water mass

The length compositions of *B. glaciale* caught in standard night tows on the six standard cruises in 1998-99 were closely similar in shape in LSW and WSW (Fig. 2). Although fewer small fish (20–30 mm) occurred in WSW than in LSW in February 1988 samples, this was likely due to sampling variation as this mode was of comparable prominence in both water masses in the length compositions from other months. A recruitment event was indicated by the occurrence in August samples of a strong mode at about 18 mm (range: 13–25 mm). These post-metamorphic age 0 fish formed the dominant mode also in October and December samples, becoming progressively less prominent in subsequent months but traceable to the mode at 37 mm, again in August samples, at age 1. Larger modes, representing older age groups, were also present, and fish up to a length of about 65 mm were not uncommon. In standard night tows overall, the largest specimen recorded was 71 mm.

Catches of *B. glaciale* in deep day tows were composed of larger fish than those caught in standard night tows. The minimum and maximum lengths in catches made in deep day tows ranged from 18–79 mm, compared to 13–71 mm in night tows. The median of minimum lengths was 31mm, compared to 25 mm in standard night tows, indicating that the smallest post-metamorphic animals were not available to the day tows. The median of maximum lengths was 65 mm, compared to 57.5 mm in standard night tows,

Table 2. Median number caught of *B. glaciale* (*B.g.*) and *C. maderensis* (*C.m.*) in deep day, tows by season and water mass. (Winter–December to April, Summer–June to October.)

| | WSW | | | LSW | | |
|---|---|---|---|---|---|---|
| Season | Number of Tows | *B.g.* | *C.m.* | Number of Tows | *B.g.* | *C.m.* |
| Winter | 13 | 68 | 3 | 15 | 204 | 12 |
| Summer | 23 | 116 | 6 | 4 | 338 | 5 |
| Ratio | | 1.7 | 2.0 | | 1.7 | 0.4 |

indicating that the largest fish in the population were not fully represented in the shallow standard night tows. These differences are illustrated by the length composition measurements from the October 1988 (N110) survey as, in that survey, standard night and deep day samples were collected in both WSW and LSW (Fig. 3).

**Larval occurrences**

About 1,000 larval *B. glaciale* (defined as animals <12 mm) were caught in ichthyoplankton surveys conducted by DFO in 1976–82 and about 13,000 larvae were caught in 1977–87 NMFS surveys. Catches occurred throughout the areas sampled (57°W-67°W by DFO, 67°W to 75°W by NMFS (Table 3)), at stations located over or adjacent to the continental slope. In both survey series, 98% of catches occurred in April–June (Table 3).

**Reproduction**

Females categorized as ripe, *i.e.* ovaries contained some translucent eggs, occurred in October, December, February and April catches, although primarily in December–February. Spent fish were noted in samples from December to June. This pattern of temporal distribution in occurrences of ripe females was noted in samples from both LSW and WSW, indicating a general coincidence in the timing and duration of spawning between water masses.

The maturity stage data from December, February and April samples were chosen for calculation of length at sexual maturation. The resulting maturity ogives for females differed between water masses (Fig. 4). Length at 50% maturity ($L_{50}$) was 32–33 mm in WSW (length range over which maturation occurred was approximately 20–45 mm) and $L_{50}$ was about 39-40 mm in LSW (maturation length range was approximately 30–55 mm).

The ratio of females exhibiting full infracaudal gland development versus those with no, or partial development, when plotted against length, gave ogives which also differed by water mass, $L_{50}$ being 31 mm in WSW and 35 mm in LSW (Fig. 4). This is in general agreement with the result of direct gonad maturity staging, maturation preceding egg development by a few millimetres in fish length. In males, gland development did not differ between water masses, $L_{50}$ occurring at 27–28 mm in both cases, suggesting that males mature at a smaller size than females.

A count was obtained of the total number of eggs in the ovaries of each of 97 ripe females. These specimens, which ranged in length from 26 to 70 mm, came predominantly from December and February samples, with a few from October (3) and April (10), and most (74%) came from stations classed as being in WSW. Fecundity averaged 583 eggs (range = 140–1098) and was significantly correlated with fish length ($r = 0.633$, $df = 95$, $p < 0.01$).

**Feeding and food composition**

Stomach fullness of *B. glaciale* varied seasonally (Fig. 5), being highest in summer (more than ½ full) and lowest in winter-spring, particularly in April when stomachs were close to empty. Much of the food in the stomachs was unidentifiable in all months but more so in February–June.

Calanoid copepods comprised almost 75% of identifiable dietary items (Table 4), followed in importance by euphausids (15–20%). Food items were of roughly similar importance in February–June 'winter' and August–December 'summer' samples except for a higher importance of *Pleuromamma* spp. in summer.

***Ceratoscopelus maderensis***

**Distribution**

The median catch per tow of *C. maderensis* was higher in WSW than it was in LSW in all surveys (Table 1). However, the differential in density between water masses

varied seasonally, being about x17 higher in WSW in winter and about x4 higher in summer (Table 2). Very few *C. maderensis* were caught in deep day tows in either season (Table 2).

**Length compositions by water mass**

The length compositions of catches in standard IYGPT night tows differed substantially between water masses. Catches in LSW were composed predominantly of large fish and those from WSW of small fish (Fig. 6).

In WSW, the August catch was composed almost exclusively of larval and immediately post-metamorphic fish with modes of 13 and 19 mm, respectively. These recruits can be followed in the length-frequencies of October and December catches as a multi-modal group extending from 15 to 40 mm. The multi-modality of

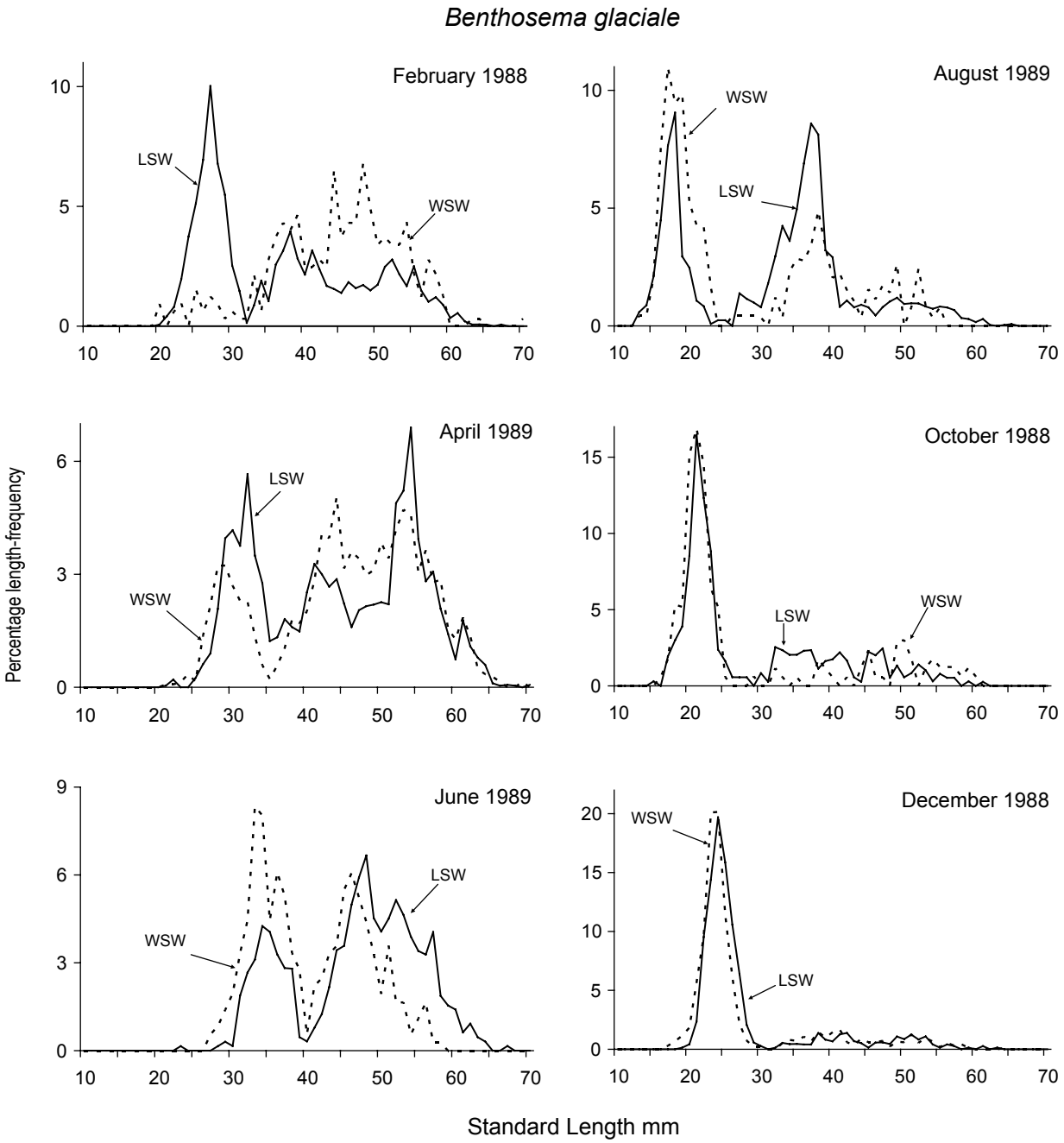


Fig. 2. Length-frequencies of *Benthosema glaciale* in standard IYGPT tows by survey and water mass.

the lengths suggests that there were several waves of spawning. By February, these groups had coalesced into a single mode at 35mm (range 25–45 mm), and this mode was observable at about 48 mm in April and June samples (ranges 35–55 mm and 40–60 mm, respectively). Although missing in August samples, this mode was observed in October catches (at 45–60 mm), but was absent thereafter, indicating a lifespan of one year in WSW.

Catches from LSW were dominated by fish larger than about 45 mm. Although recruiting post-metamorphic fish formed a substantial proportion of catch numbers in August, few were caught in October and none in December. Some fish of this age group reoccurred at 30–45 mm in February samples, but not in April. The February occurrence was likely an assignment error caused by the difficulties in assigning water mass to tows made in the large transition area that existed in that month. The mode in the length frequency of large fish at 45–55 mm in August samples progressed in subsequent months to about 55–65 mm in April. However, in June, this modal length group was smaller, at 45–60 mm, and overlapped that in WSW, suggesting a transfer of young-of-the-year fish from WSW to LSW at this time. It is in this month also that catch rates were highest in LSW (Table 1), supporting such a conclusion.

The length ranges of the *C. maderensis* caught in deep IYGPT day tows reflected the dichotomy in the length distributions observed in standard night catches. The

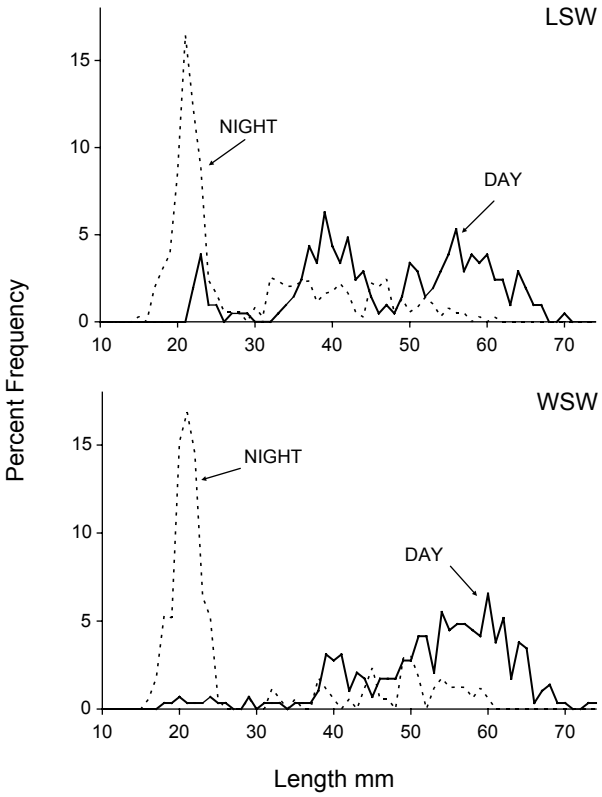


Fig. 3. *Benthosema glaciale:* relative length-frequencies of catches in deep day tows compared to those in standard night tows in LSW and WSW in October 1988 (N110).

Table 3. Percentage distribution, by month and by longitude, of catches of larval *B. glaciale* and *C. maderensis* in DFO and NMFS ichthyoplankton surveys. (+, less than 0.5%; Latitude 57° = 56°00' – 57°59', etc; dots indicate no sampling.)

| Series | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ***Benthosema glaciale*** | | | | | | | |
| DFO | 0 | 0 | 0 | 59 | 30 | 9 | 2 | + | + | 0 | 0 | 0 |
| NMFS | + | 0 | 1 | 38 | 53 | 7 | + | + | + | + | 0 | + |
| | | | | | ***Ceratoscopelus maderensis*** | | | | | | | |
| DFO | 0 | 0 | 0 | 0 | 11 | 24 | 38 | 16 | 1 | 10 | 0 | 0 |
| NMFS | + | + | + | + | 8 | 5 | 11 | 10 | 29 | 30 | 5 | + |

| Series | 75° | 73° | 71° | 69° | 67° | 65° | 63° | 61° | 59° | 57° |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ***Benthosema glaciale*** | | | | | |
| DFO | … | … | … | … | 26 | 13 | 10 | 42 | 7 | 2 |
| NMFS | 31 | 33 | 15 | 8 | 13 | … | … | … | … | … |
| | | | | | ***Ceratoscopelus maderensis*** | | | | | |
| DFO | … | … | … | … | 13 | 86 | + | 1 | + | 0 |
| NMFS | 11 | 17 | 32 | 23 | 17 | … | … | … | … | … |

medians of the minimum and maximum lengths in WSW day tows were 29 mm and 38 mm but, in LSW day tows, were 55 mm and 59 mm. The largest specimen recorded overall was 75 mm. It was caught in a standard night tow in WSW during exploratory cruise N067 in August 1986.

**Larval occurrences**

The DFO ichthyoplankton surveys caught about 2000, and NMFS surveys caught about 43 000 *C. maderensis* larvae (animals <18 mm), predominantly over the continental slope. Almost all the larvae caught in DFO surveys were from stations at 64–68°W, *i.e.* at the most western part of the DFO sampling area (Table 3). In NMFS surveys, however, catches of larvae occurred in abundance from Georges Bank to Cape Hatteras (Table 3). Larvae were recorded from May to October in DFO surveys whereas in NMFS surveys substantial quantities were caught also in November and a few were recorded in December–April, indicating some spawning year-round off the USA coast (Table 3).

**Reproduction**

The spawning season, as defined by the occurrence in samples of females with ripe eggs, extended from April to October, such occurrences being most frequent in June and August samples. This gonad development occurred in specimens from LSW as well as in those from WSW.

Fish with gonads sufficiently developed for sex to be determined were first noted at about 25 mm in length and essentially all fish larger than 35 mm could be sexed. The smallest female classified as ripening was 44 mm, but most in ripening/ripe/spent stages were greater than 55 mm (Fig. 7). The maturity ogive for females, based on April–August data, was similar in LSW and WSW (Fig. 7). (As noted previously, no inferences could be made regarding size at maturity of males.)

A count was obtained of the total number of eggs in the ovaries of each of 33 ripe females. These specimens, which ranged in length from 58 to 70 mm, came predominantly from June and August samples, with a few from April (2) and October (5). Sampling was divided equally between WSW (17 fish) and LSW (16 fish). Fecundity averaged 5569 eggs (range = 2134–9632). Fish length explained only 14% of this variation ($r = 0.368$, $df = 31$, $p < 0.05$).

The prolonged spawning season, the fact that all fish large enough to spawn do not do so at the same time (Fig. 7), and the lack of correlation between number of eggs and fish length, indicate that individual fish spawn several times during the spawning season.

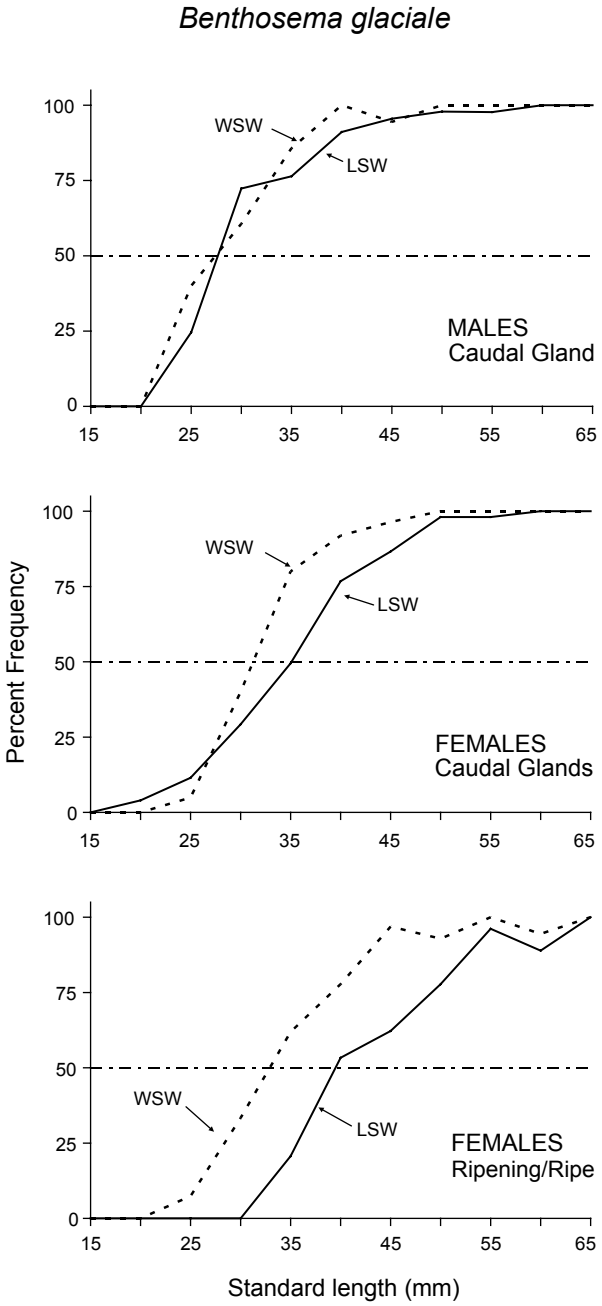


Fig. 4. *Benthosema glaciale*: caudal gland development with length in males (top) and females (middle) based on all samples), and percentage frequency of ripening and ripe females by length in December to April samples (bottom). (Lengths are midpoints of 5 mm length groups.)

**Feeding and food composition**

Stomach fullness was greater than 50% (index >2.0) in all months. There was, nonetheless, some evidence for a maximum in fullness in August and a minimum in April

and for a coincident inverse trend in the extent to which the contents were digested (Fig. 5).

Calanoid copepods were the most important dietary contributors overall, comprising about 50% of specimens observed, amphipods, euphausids and chaetognaths accounting, almost equally, for most of the remainder (Table 5). Most food items were of importance in both winter and summer except that chaetognaths contributed to diet mainly in winter (Feb.–June) and gastropods (likely pteropods) mainly in summer (Aug.–Dec.).

## Discussion

### *Benthosema glaciale*

*Benthosema glaciale* has a North Atlantic sub-polar – temperate distribution (Backus *et al.*, 1977). In the Western Atlantic, it has been recorded as far north as the Davis Strait (Sameoto, 1989) and accounted for about 95% of the myctophid specimens in the collections of Backus *et al.* (1977) and McKelvie (1985a) from subarctic waters east of Grand Bank. McKelvie (1985b) found that *B. glaciale* predominated also in mesopelagic fish samples from mixed water masses southwest of Grand Bank, *i.e.* in the northeastern part of the Slope Sea. Based on present samples, Themelis and Halliday (2012) confirmed the predominance of this species in the LSW that occupies much of the northeastern portion of the Slope Sea, but found that the species ranked only third in abundance in catches made southwest of the LSW/WSW boundary. The species distribution in the eastern Atlantic similarly extends from arctic to temperate waters, including the Mediterranean Sea (*e.g.* Olivar *et al.*, 2012).

The present analysis shows that the density of *B. glaciale* was substantially higher in LSW than in WSW in all seasons, based on standard night tows. The lower differentials in density between water masses observed in samples from February and April, compared to other months, may indicate seasonal differences, but the number of samples was small and the differences may be sampling anomalies. Catch rates in deep day tows also were higher in LSW than in WSW, but the difference between median catches was less, x3 on average, regardless of season. There was a difference also in the size compositions of the populations caught at different depths, catches in deep day tows being predominated by large animals, greater than 30mm, in contrast to shallow night tows, in which animals smaller than that, particularly those that were young of the year, were prominent.

Samples from standard cruises reflect conditions in the general proximity of the boundary between LSW and

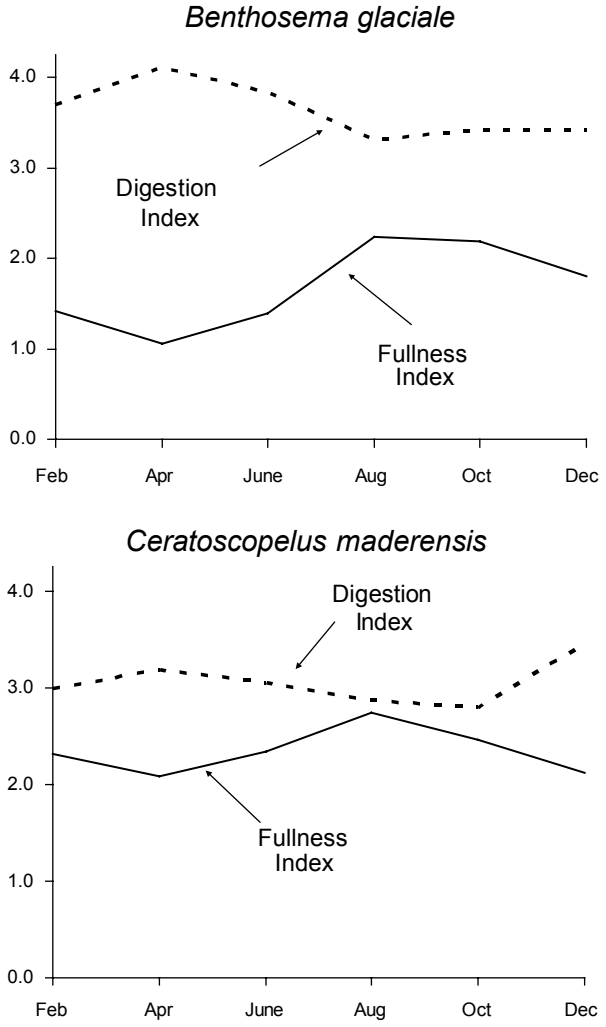


Fig. 5. Indices of stomach fullness and of the extent of digestion of stomach contents by sampling month for *B. glaciale* and *C. maderensis.*

WSW and thus present data may minimize the differences in abundance between the water masses overall. The earlier exploratory cruises, which included samples from more eastern areas (Fig. 1), showed higher differentials in catch rates in LSW vs. WSW. No sampling was conducted during the present study in areas to the west of the standard sampling area. However, Backus and Craddock (1977) recorded high catches of *B. glaciale* in more western parts of WSW also, suggesting that present data can be taken as indicative of WSW more generally. Gartner *et al.* (2008) reported captures of adults at the southernmost extent of WSW off Cape Hatteras (about 35°N), and the captures of larval stages along the entire continental slope to Cape Hatteras, indicate that *B. glaciale* is capable of completing its life cycle throughout WSW as well as in LSW. Transport of specimens of *B. glaciale* into semi-

subtropical waters south of the Gulf Stream in cold-core rings has been reported but available evidence indicates that the species does not reproduce there (Backus and Craddock, 1982; Karnella, 1987).

The size composition of catches was similar in WSW and LSW, suggesting that annual recruitment success and subsequent growth rates were similar in the two areas. A lifespan of 4–5 years was determined, using otolith ring counts, by Halliday (1970) for fish caught over the Nova Scotia continental slope. It appears, however, that the population sampled by Halliday (1970) did not include the full size/age range of the Slope Sea population. His largest specimen had a standard length of 67 mm, whereas Sameoto (1988) subsequently reported an 83 mm specimen from the same slope area and fish up to 79 mm were caught in present samples collected over adjacent oceanic depths. Gjøsæter (1981) reported captures of this species in Norwegian waters that were in the 70–80 mm length range and as old as 7–8 years, and present data

Table 4. Stomach contents of *Benthosema glaciale* by season, and overall, as percentages of the total number of identifiable items. (+ indicates less than 0.5%. *–indicates not found in *C. maderensis*.)

| Taxon | % Feb.–June | % Aug.–Dec. | % All |
|---|---|---|---|
| **Copepoda** | 1.9 | 0.9 | 1.4 |
| **Calanoida** | 18.1 | 18.8 | 18.5 |
| *Candacia* spp. | 1.0 | 0.9 | 1.0 |
| *Candacia armata* | 2.4 | + | 1.3 |
| *Candacia pachydactyla* | + | – | + |
| *Euchaeta norvegica* | 7.2 | 2.1 | 4.6 |
| *Metridia* sp. | 21.0 | 19.5 | 20.2 |
| *Pleuromamma* spp. | 3.9 | 27.5 | 15.8 |
| *Pleuromamma robusta* | 6.0 | 7.5 | 6.8 |
| *Pleuromamma xiphaes* | + | + | + |
| *Pleuromamma borealis* | + | 0.5 | + |
| *Rhincalanus nasutus* | 0.5 | + | + |
| *Euchirella rostrata* | 5.3 | 0.7 | 3.0 |
| *Aetideus armatus* | + | + | + |
| **Amphipoda** | 1.0 | 0.5 | 0.7 |
| **Gammaridea** | + | + | + |
| *Lysianassidae | + | + | + |
| **Hyperiidea** | + | + | + |
| *Themisto* sp. | 1.0 | 0.7 | 0.8 |
| *Themisto gaudichaudi* | 7.0 | 2.4 | 4.6 |
| **Malacostraca** | – | – | – |
| Euphausiidae | 8.7 | 2.4 | 5.5 |
| Euphausid furcilia ns | + | + | + |
| *Thysanoessa* spp. | 1.4 | 0.5 | 1.0 |
| *Thysanoessa raschii* | 2.4 | 4.7 | 3.6 |
| *Thysanoessa longicaudata* | 9.2 | 6.1 | 7.6 |
| **Ostracoda** | 0.7 | 2.1 | 1.4 |
| **Decapoda** | – | + | + |
| **Gastropoda** | – | + | + |
| **Pisces** | – | 0.7 | + |

indicate that similar lengths and ages are attained off Nova Scotia. The largest length recorded for the species is 98.5mm SL (estimated total length: 103 mm) for a specimen caught off Norway and estimated by Gjøsæter (1973) to be 7–8 years old.

In both water masses, spawning occurred in winter and larvae were most abundant in the plankton in April–May, at least along the continental slope. Post-metamorphic fish were first caught in the IYGPT net in August at about 18 mm and lengths progressed to about 20–30 mm by the following winter at age 1. However, there were differences between water masses in size at maturity, females in WSW maturing at a smaller size than those in LSW. In WSW, the maturity ogive included fish that were in the 20–30 mm size range, indicating that some age 1 and most age 2 fish matured. In LSW, however, essentially no age 1 females, and less than half of age 2 females were large enough to

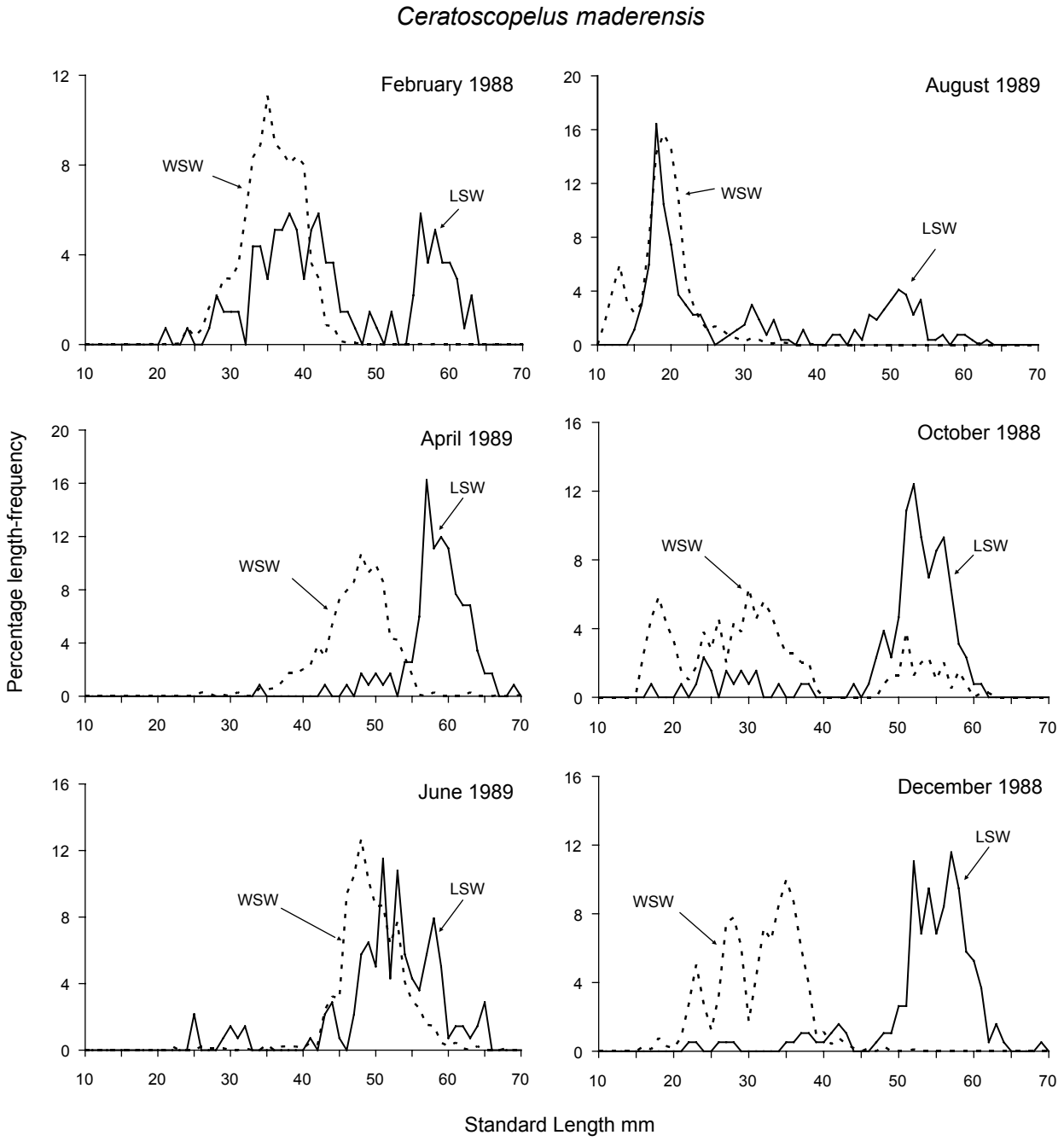


Fig. 6. Length-frequencies of *C. maderensis* in standard IYGPT tows by survey and water mass.

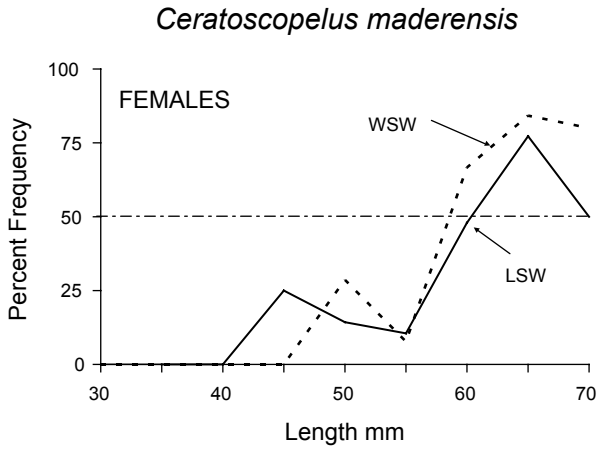


Fig. 7. *C. maderensis*: percentage frequency of ripening and ripe females by length in April to August samples. (Lengths are midpoints of 5 mm length groups.)

spawn, as found to be the case for specimens from the Nova Scotia continental slope by Halliday (1970) and east of Grand Bank by Albikovskaya (1988). However, the time of spawning differed in Norwegian waters, ripe and spawning fish occurring most commonly in May and June (Gjøsæter, 1981).

Fecundity averaged 583 eggs ($N = 97$, range = 140–1098) in fish of 26–70 mm in length. These estimates are lower than those of Gjøsæter (1981), who found that specimens collected off Norway had an average fecundity of 781 eggs ($N = 28$, range = 162–1940) in fish of 45–70 mm. Fecundity was significantly correlated with fish length in both cases.

Sameoto (1988) found that the diet of *B. glaciale* over the Nova Scotia continental slope, adjacent to the present sampling area, was even more dependent on copepods than was the case in present data. The dominant food items in his collections were *Calanus* species. Diet studies of *B. glaciale* off eastern Grand Bank-Flemish Cap (Albikovskaya, 1988; García-Seoane *et al*, 2013) and in the western Labrador Sea (Pepin, 2013) also found *Calanus*, particularly *C. finmarchicus*, to be predominant, but sampling in these studies was also conducted along the continental slope. The most likely explanation for the absence of *Calanus* in the diet of the specimens examined in the present study is that members of this genus did not occur in the oceanic waters sampled. The minimum in stomach fullness in winter samples may indicate reduced feeding opportunities during that season.

***Ceratoscopelus maderensis***

*Ceratoscopelus maderensis* has a North Atlantic temperate distribution. Although initially thought to inhabit semi-subtropical waters also (Backus *et al*., 1977), subsequent evidence of the importance of cold-core rings in transporting Slope Sea species south into the Sargasso Sea caused Backus and Craddock (1982) to conclude that the species was better classed as temperate only, a conclusion supported by Karnella (1987), who caught only juveniles in sampling off Bermuda.

Themelis and Halliday (2012) found that this species ranked first in abundance in catches made in the temperate waters south-west of the LSW/WSW boundary, but found also that it ranked second in catches from the colder water to its northeast. The present analysis of data from standard night tows shows that there was a differential in density between water masses of about five to one, on average, in WSW vs. LSW. The differential was less in summer (June–October) than in winter. Few specimens of this species were caught in deep day tows, so standard night tows can be taken as reflective of the population as a whole. Occurrences in LSW were not limited to the area immediately adjacent to the boundary with WSW but were wide-ranging within the LSW area, as shown by the initial exploratory surveys, and previously by McKelvie (1985, a & b). Occurrences were common in McKelvie's (1985b) samples from the Gulf Stream also, but few were caught in his samples from the Newfoundland Basin, east of Grand Bank.

There was a dichotomy in the size compositions between animals caught in WSW vs. LSW, those in WSW being generally less than 50mm in length and those in LSW being larger than that. The largest specimen recorded, at 75 mm, although caught in WSW, was taken close to the WSW/LSW boundary. Large *C. maderensis* have been reported previously as occurring also along the continental slope. Halliday and Scott (1969) caught fish as large as 70 mm along the Scotian Shelf slope, adjacent to the present sampling area. More significant, however, are the reports of Backus *et al.* (1968) of shoals of 52–73 mm fish over the continental slope south of New England (39°48'N, 70°33'W), and of Gartner *et al.* (2008) observing near-bottom aggregations of 54–74 mm fish over the continental slope off Cape Hatteras. Thus, large specimens appear to be associated with marginal environments.

In a study of Northeast Atlantic populations of this species, Linkowski *et al.* (1993) determined a life-span of two years, with a high mortality occurring after spawning in the first year. They noted also some geographic segregation, younger fish being largely absent from the northern and northeastern parts of their sampling area. The largest fish they recorded was 76 mm. Present data indicate that the life history in the northwestern Atlantic population exhibits a pattern very similar to that in the northeastern Atlantic, showing a segregation of age

Table 5. Stomach contents of *Ceratoscopelus maderensis* by season, and over all, as percentages of the total number of identifiable items. (+ indicates less than 0.5%. *– indicates not found in *B. glaciale*.)

| Taxon | % Feb.–June | % Aug.–Dec. | % All |
|---|---|---|---|
| **Copepoda** | 0.9 | 0.7 | 0.8 |
| **Calanoida** | 15.9 | 8.3 | 13.7 |
| *Candacia* spp. | 0.6 | 1.3 | 0.8 |
| *Candacia armata* | 0.8 | 0.7 | 0.8 |
| *Candacia pachydactyla* | + | 3.6 | 1.1 |
| **Centropages typicus* | + | – | + |
| *Euchaeta norvegica* | 2.4 | 0.7 | 1.9 |
| *Metridia* sp. | 17.5 | 13.3 | 16.3 |
| *Pleuromamma* spp. | 8.5 | 4.7 | 7.4 |
| *Pleuromamma robusta* | 3.2 | 3.3 | 3.2 |
| *Pleuromamma xiphaes* | 1.0 | + | 0.8 |
| *Pleuromamma borealis* | 1.1 | 1.6 | 1.3 |
| *Rhincalanus nasutus* | 0.6 | – | 0.5 |
| **Acartia hudsonica* | + | – | + |
| *Euchirella rostrata* | 1.8 | 0.9 | 1.5 |
| *Aetideus armatus* | + | 0.6 | + |
| **Amphipoda** | 1.0 | 1.1 | 1.0 |
| **Gammaridea** | + | + | + |
| **Hyperiidea** | 1.2 | 1.7 | 1.3 |
| *Themisto* sp. | 1.8 | 2.2 | 1.9 |
| *Themisto gaudichaudi* | 7.9 | 14.5 | 9.8 |
| **Hyperia galba* | + | – | + |
| **Malacostraca** | – | – | |
| Euphausiidae | 2.4 | 3.2 | 2.6 |
| Euphausid furcilia[1] | 3.1 | 1.7 | 2.7 |
| *Thysanoessa* spp. | 0.8 | 0.7 | 0.8 |
| *Thysanoessa raschii* | 0.9 | 6.2 | 2.4 |
| *Thysanoessa longicaudata* | 1.8 | 3.0 | 2.1 |
| **Meganyctiphanes norvegica* | + | – | + |
| **Euphausia krohnii* | + | 6.9 | 2.3 |
| **Ostracoda** | 2.5 | 6.0 | 3.5 |
| **Decapoda** | + | + | + |
| **Gastropoda** | + | 11.6 | 3.6 |
| ***Chaetognatha** | 11.4 | + | 8.1 |
| **Sagitta* sp. | 8.6 | + | 6.1 |
| ***Ctenophora** | + | – | + |
| **Pisces** (incl. scales) | + | + | + |

[1] Includes 6 identified as *Thysanoessa raschii* and 13 as *Thysanoessa longicaudata*.

groups, those caught in WSW being 1yr olds and in LSW being primarily 2 yr. olds.

The reproductive contribution of the LSW component of the population is not clear. The large females caught in LSW matured sexually and contributed to spawning. However, those fish examined were from samples taken immediately adjacent to the LSW/WSW boundary and were not necessarily representative of the LSW population as a whole. Post-larval specimens occurred in LSW samples irregularly and only in small numbers, and these could have been transported from WSW due to mixing in the boundary area. Historical ichthyoplankton surveys showed larval occurrences over the continental slope from 64°W (the western end of the Scotian Shelf) south to Cape Hatteras. Only a few specimens were taken, late in the spawning season (Sept.–Oct.), from the more northeastern part of the Scotian Shelf adjacent to the present sampling area, suggesting that there was little spawning activity in that area. It is possible that those large animals caught in the central and eastern parts of LSW, and along the Nova Scotia continental slope, are expatriates, making no reproductive contribution, as described by Zurbrigg and Scott (1972) for Northwest Atlantic populations of *Myctophum punctatum*.

There are no studies of the diet of *C. maderensis* in the NW Atlantic comparable to present data (although Podrazhanskaya (1993) gave some general information from a sample taken east of Grand Bank that is not in conflict with present results). There was a fairly strong commonality in diet with *B. glaciale*, the similarity being about 65%. However, this is an overestimate as the comparison includes data at taxonomic levels above species. There was some seasonal variation in stomach fullness but it was less marked than that observed in *B. glaciale*.

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The Journal is for the primary publication of original practical and theoretical research that is unpublished and is not being submitted for publication elsewhere. While it is intended to be regional in scope, papers of general applicability and methodology may be considered. Space is also provided for notes, letters to the editor and notices. Each paper is assigned to an Associate Editor of the Journal's Editorial Board, and is normally reviewed by two referees regarding suitability as a primary publication.

**NAFO Scientific Council Studies**

The Studies publishes papers which are of topical interest and importance to the current and future activities of the Scientific Council, but which do not meet the high standards or general applicability required by the Journal. Such papers have usually been presented as research documents at Scientific Council meetings and nominated for publication by the Standing Committee on Publications. Studies papers are not peer reviewed.

## Content of Paper

The paper should be in English. The sequence should be: Title, Abstract, Text, References, Tables and Figures.

**Title**

The paper should start with the title, followed by the name(s), address(es) and emails of the author(s) including professional affiliation, and any related footnotes.

**Abstract**

An informative concise abstract should be provided along with key words listed alphabetically.

**Text**

In general, the text should be organized into Introduction, Materials and Methods, Results, Discussion, and Acknowledgements. Authors should be guided by the organization of papers that have been published in the NAFO Journal or Studies.

**Introduction** should be limited to the purpose and rationale of the study.

**Materials and Methods** should describe in sufficient detail the materials and methods used, so as to enable other scientists to evaluate or replicate the work.

**Results** should answer the questions evolving from the purpose of the study in a comprehensive manner and in an orderly and coherent sequence, with supporting tables and figures.

**Discussion** should explain the main contributions from the study, with appropriate interpretation of the results focusing on the problem or hypothesis. Comparisons with other studies should be included here.

**Acknowledgements** should be limited to the names of individuals who provided significant scientific and technical support, including reviewers, during the preparation of the paper, and the names of agencies which provided financial support.

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The references cited in the text should be listed alphabetically. References should be mainly restricted to significant published literature. Unpublished documents and data, papers in preparation, and papers awaiting acceptance to other journals, may be cited with full contact addresses as unpublished or personal communications.

***Examples:***

KING, M. 1995. Fisheries biology, assessment and management. Fishing News Books, UK, 341 p.

CROWDER, L. B., and S. A. MURAWSKI. 1998. Fisheries by-catch: implications for management. *Fisheries*, **23**: 8–16. doi:10.1577/1548-8446(1998)023<0008:FBIFM>2.0.CO;2

ÁVILA DE MELO, A. M., D. POWER, and R. ALPOIM. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc.*, No. 52, Serial No. N5138, 19 p.

Text citations of the above would be (King, 1995; Crowder and Murawski, 1998; Ávila de Melo *et al.*, MS 2005). The surnames of two authors may be used in a citation, but *et al.* should be used for more than two authors. The citation of mimeographed reports and meeting documents should contain the abbreviation "MS". Abbreviations of periodicals can be found ftp://ftp.fao.org/fi/asfa/Monitoring_List/MASTER.txt . The Digital Object Identifier (doi) should be included if available. http://www.crossref.org/freeTextQuery/ can be used to checked this.

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**All figures should be submitted as separate files in .eps or .ps format.** Photographs, maps and contour plots can also be submitted in high quality .jpg format.

If using excel, open the files in R and save the graphs by right clicking and saving as metafiles or postscript files. If using SlideWrite copy the files as Metafiles (WMF). Do not save them as bitmap files. They are not editable.

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